

REVISION OF THE CRINOID FAMILY COMASTERIDÆ, WITH DESCRIPTIONS OF NEW GENERA AND SPECIES.

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The work of the steamer *Albatross*, of the United States Bureau of Fisheries, especially within the last two years, has resulted in the accumulation of a magnificent collection of comasterid material, practically every known and numerous heretofore unknown species being represented. This has been studied in connection with the remarkably comprehensive collection belonging to the zoological museum of the University of Copenhagen (previously studied by Drs. C. F. Lütken and P. H. Carpenter), for the privilege of examining which I am indebted to the generosity of my friend, Dr. Th. Mortensen; with the very fine collection of Japanese comasterids deposited in the U. S. National Museum by Mr. Frank Springer; with the collection made by the German steamer *Gazelle* in Australia, sent to me for study through the kindness of Drs. W. Weltner and R. Hartmeyer, and with the collections of a number of American museums. Still other collections have been examined at different times, and the notes made on them have proved of considerable value, the most important of these being the collection at the Museum of Comparative Zoology, which contains specimens identified by Carpenter, and that of the Boston Society of Natural History.

After the completion of the work on this "revision," the authorities of the Indian Museum at Calcutta, through the superintendent, Dr. N. Annandale, sent me the specimens collected by the steamer *Investigator*, which proved to be a collection of more than usual interest. It was with considerable gratification that I found, after a critical study of the *Investigator* material, no changes of any kind were necessary, and I was thereby induced to publish the "revision" in its present form, believing that, if such a large collection as that of the *Investigator* did not alter in any way the general scheme, there was a reasonable hope of at least as long a life as is enjoyed by most "revisions."

The history of the family Comasteridæ may be said to date from that most excellent memoir of Dr. P. H. Carpenter on the genus *Actinometra*. In this memoir he gives a detailed account of the systematic treatment of the various species of the genus by previous authors, and ably reduces to order a systematic chaos scarcely surpassed in the whole subject of zoology; for even so great a zoologist as Prof. Johannes Müller, in the only monograph then published on the unstalked crinoids, had placed a single species (under four different specific names) under the subgenus *Actinometra* among the exocyclic forms (twice); under the subgenus *Alecto* among the endocyclic forms, and again under the subgenerically *incertæ sedis*, in the heterogeneous group *Comatula*.

Since 1879 the genus *Actinometra* has been accepted in the sense in which it was used by Carpenter. Nine years afterwards he split it up into eight specific groups, distributing these among four "series," and this arrangement has been used ever since. Shortly afterwards the genus was raised to family rank, on a par with the family "Antedonidæ," covering the genus "*Antedon*" of Doctor Carpenter. This I have recently shown to be an unnatural division. In the course of my work I found the genus *Actinometra* becoming somewhat unwieldy, and I accordingly split it in two sections, one small and one large; but with the accession of new material the large division proved not to be natural, and I split that into two parts. Enormous collections from the Philippine Islands having been received, a still further change was seen to be necessary, and the last of the divisions created was shattered into three fragments. I discarded the appropriate and euphonious name *Actinometra* proposed by Professor Müller in favor of *Comatula* of Lamarek, of which it is a pure synonym, with the same type. While the name Comatulidæ was first employed to cover the family in place of Actinometridæ (not available because of the disuse of *Actinometra*), I soon found that confusion with the Comatuladæ of Fleming (1828) and Comatulidæ of d'Orbigny (1852) and succeeding authors, with a more or less comprehensive range of meaning, but never so restricted as to cover the "Actinometridæ" alone, made a change desirable, and I therefore substituted "Comasteridæ," the name being derived from that of the next oldest genus.

The most important discovery made in regard to the Comasteridæ since the publication of Carpenter's memoir in 1879 is that of Mr. Frank Springer, who in 1903 described and figured a strongly developed ambulacral plating on the arms and pinnules of a new species from the Tortugas. I have since found these plates to be universally present in the species of the "Fimbriata group" from the West Indies, well developed even in "*Actinometra*" *lineata*, in which I detected it in some of the *Challenger* specimens previously examined by

Carpenter. These plates appear to represent the side plates of the Pentacrinitidæ, Tropiometridæ, Thalassometridæ, Antedonidæ, etc., although performing the function of both side and covering plates. The latter are phylogenetically more advanced structures; whereas side plates are phylogenetically the thin produced ventrolateral border of the pinnulars and brachials which has become separated from the parent ossicle by suture, so covering plates are the produced inner distal angles of the side plates which have become secondarily separated off.

KEY TO THE GENERA OF THE COMASTERIDÆ.

- a*¹. Six pinnules following the first pair absent; mouth always central.
(1) COMATILIA.
- a*². All pinnules present; mouth usually more or less eccentric.
- b*¹. IBr₁ and ₂ and first two joints after each axillary united by syzygy.
(2) COMATULA.
- b*². IBr₁ and ₂ and first two joints after the first axillary united by synarthry.
- c*¹. Cirri present.
- d*¹. Cirri without dorsal spines (ten arms).
- e*¹. First two pinnules much stouter than the succeeding; cirri long, slender, and numerous (XL)----- (3) COMINIA.
- e*². First two pinnules more slender than the succeeding; cirri short and stout, few in number (to XXVII)----- (4) COMACTINIA.
- d*². Cirri with dorsal spines or projections (ten or more arms).
- e*¹. Distal pinnules exceedingly slender with greatly elongated joints which have expanded articulations; ten arms-- (5) LEPTONEMASTER.
- e*². Distal pinnules comparatively stout, the joints rarely over twice as long as broad, the articulations not expanded.
- f*¹. Ten arms; synarthrial tubercles prominent; pinnule joints with the distal ventro-lateral angle produced----- (6) COMISSIA.
- f*². More than ten arms; synarthrial tubercles not developed; no production of the distal ventro-lateral angles of the pinnule joints.
- g*¹. First brachial bearing a pinnule on arms arising from a IBr or subsequent axillary; a syzygy between the second and third brachials.
- h*¹. Brachials in distal half of arm exceedingly short, almost discoidal; ambulacra naked----- (7) CAPILLASTER.
- h*². Brachials in distal half of arm triangular or very obliquely wedge-shaped, nearly or quite as long as broad; pinnule ambulacra with large side plates----- (8) NEMASTER.
- g*². First brachial never bearing a pinnule.
- h*¹. All division series 2; a syzygy between the first two brachials----- (9) COMATELLA.
- h*². Several or all of the division series 4 (3+4).
- i*¹. Proximal pinnules more slender than the succeeding; combs occur at intervals on the distal pinnules-- (10) COMASTER.
- i*². Proximal pinnules stouter than the succeeding; no combs on the distal pinnules----- (11) COMANTHUS.
- e*². Cirri absent; centro-dorsal a thin pentagonal or stellate plate.
- d*¹. First brachial bearing a pinnule; first syzygy between the first two brachials----- (7) CAPILLASTER.

*d*². First brachial never bearing a pinnule.

*e*¹. Proximal pinnules more slender than the succeeding; terminal comb short, with long curved teeth, appearing at intervals along the distal pinnules.----- (10) COMASTER.

*e*². Proximal pinnules stouter than the succeeding; terminal comb long with short rounded teeth, confined to the proximal pinnules.

(11) COMANTHUS.

SUPPLEMENTARY KEY TO GENERA CONTAINING SPECIES WITH TEN ARMS ONLY.

*a*¹. Six pinnules following the first pair absent; large side plates developed along the pinnule ambulacra; opposing spine forked or branched.

(1) COMATILIA.

*a*². All pinnules present; no ambulacral plating; opposing spine single.

*b*¹. 1Br₁ and ₂ and first two brachials united by syzygy----- (2) COMATULA.

*b*². 1Br₁ and ₂ and first two brachials united by synarthry.

*c*¹. Cirri without dorsal spines or projections.

*d*¹. First two pinnules much stouter than the succeeding; cirri long, slender, and numerous (XL)----- (3) COMINIA.

*d*². First two pinnules more slender than the succeeding; cirri short and stout, few in number (to XXVII)----- (4) COMACTINIA.

*c*². Cirri with dorsal spines or projections.

*d*¹. Distal cirrus joints (except the penultimate) considerably longer than broad; synarthrial tubercles not developed; distal pinnules exceedingly slender, with greatly elongated joints which have expanded articulations----- (5) LEPTONEMASTER.

*d*². Distal cirrus joints considerably broader than long; synarthrial tubercles prominent; distal pinnules comparatively stout, the joints rarely over twice as long as broad, the articulations not expanded----- (6) COMISSIA.

SUPPLEMENTARY KEY TO GENERA CONTAINING MULTIBRACHIATE SPECIES.

*a*¹. 1Br₁ and ₂ and first two joints beyond each axillary united by syzygy.

(2) COMATULA.

*a*². 1Br₁ and ₂ and first two joints beyond the first axillary united by synarthry.

*b*¹. First brachial bearing a pinnule; first brachial syzygy between the second and third brachials.

*c*¹. Brachials in distal half of arm exceedingly short, almost discoidal; ambulacra naked----- (7) CAPILLASTER.

*c*². Brachials in distal half of arm triangular or very obliquely wedge-shaped, nearly or quite as long as broad; pinnule ambulacra with large side plates----- (8) NEMASTER.

*b*². First brachial never bearing a pinnule.

*c*¹. Division series all 2; first brachial syzygy between the first two brachials on all but the outermost arms----- (9) COMATELLA.

*c*². Several or all of the division series 4 (3+4).

*d*¹. Proximal pinnules more slender than the succeeding; combs occur at intervals along the distal pinnules----- (10) COMASTER.

*d*². Proximal pinnules stouter than the succeeding; no combs on the distal pinnules----- (11) COMANTHUS.

1. Genus COMATILIA A. H. Clark.

1909. *Comatilia* A. H. CLARK, Proc. U. S. Nat. Mus., XXXVI, p. 365.

Genotype.—*Comatilia iridometriformis* A. H. Clark (new species).

Distribution.—Only known from between the Bahama Islands and Cape Fear, North Carolina.

Depth.—Two hundred and eighty fathoms.

2. Genus COMATULA Lamarck (emended).

1758. *Asterias* (part) LINNÆUS, Syst. Nat., 10th ed., II, p. 663.

1772. *Asteria* (part) BRÜNNICH, Zoölogia fundamenta, p. 230 (emendation).

[1812. *Comatule* (part) LAMARCK, Extrait du cours de zoölogie du mus. d'hist. nat. sur les animaux sans vertèbres, p. 35 (no definition)].

1816. *Comatula* LAMARCK, Hist. nat. des animaux sans vertèbres, II, p. 530, emended 1908—A. H. CLARK, Proc. U. S. Nat. Mus., XXXIII, p. 685.

1841. *Actinometra* J. MÜLLER, Archiv für Naturgesch., 1841, I, p. 140.

Genotype.—*Comatula solaris* Lamarck (new species).

Distribution.—Northern Australia to the Mergui Archipelago, China, and the Philippine Islands, ? Madagascar, ? Society Islands.

Depth.—Littoral and sublittoral.

3. COMINIA, new genus.

1908. *Comanthus* (part) A. H. CLARK, Proc. Biol. Soc. Washington, XXI, p. 220.

Genotype.—*Comanthus decameros* A. H. Clark, 1908.

Description.—Centro-dorsal discoidal, bearing numerous marginal cirri in roughly three irregular and crowded more or less alternating rows.

Cirri XL, 16–17; first joint very short, second slightly longer than broad to about twice as long as broad, third–sixth two and one-half to three times as long as broad, the following decreasing in length, the last two being squarish; opposing spine represented by a low tubercle; no dorsal spines or projections; terminal claw about as long as the penultimate joint, moderately stout and moderately curved.

Ends of the basal rays very prominent in the angles of the calyx; radials concealed; IBr₁ short, oblong, widely separated laterally; IBr₂ (ax) broadly pentagonal, about twice as broad as long.

Ten arms; first seven or eight brachials slightly wedge-shaped, then triangular about as broad as long. Arms rugged and tubercular basally, but not enlarged or swollen.

P₁ long, stout basally but becoming slender and flagellate distally; P₂ slightly smaller and slightly less stout basally; following pinnules shorter and more slender, the distal pinnules increasing to about the length of P₁; comb confined to PP_{1, 2}, and ₃.

Distribution.—Only known from the Korean Straits.

Depth.—One hundred and seventy fathoms.

4. COMACTINIA, new genus.

1840. *Comatula* (part) J. MÜLLER, Archiv für Naturgesch., 1840, I, p. 311.
 1841. *Alecto* (part) J. MÜLLER, Archiv für Naturgesch., 1841, I, p. 143.
 1849. *Comatula* (*Alecto*) J. MÜLLER, Abhandl. d. k. preuss. Akad., 1847, p. 250.
 1878. *Antedon* (part) POURTALÈS, Bull. Mus. Comp. Zool., V, p. 214.
 1881. *Actinometra* (part) P. H. CARPENTER, Bull. Mus. Comp. Zool., IX, No. 4, p. 154.
 1908. *Comaster* (part) A. H. CLARK, Proc. U. S. Nat. Mus., XXXIII, p. 685.
 1908. *Phanogenia* (part) A. H. CLARK, Proc. U. S. Nat. Mus., XXXV, p. 124.

Genotype.—*Alecto echinoptera* J. Müller, 1841.

Description.—Centro-dorsal rather large, discoidal, the cirri arranged in a single marginal row.

Cirri short and stout, IX–XXVII, 8–12; basal joints short, then two or three half again to twice as long as broad, the following decreasing in length, being about as long as broad distally; opposing spine, small, erect, median in position; no dorsal spines or projections; terminal claw about as long as the antepenultimate joint (which is longer than the penultimate) stout and strongly curved basally, becoming slender and nearly straight distally.

Ends of the basal rays visible in the interradian angles; radials concealed; IBr_1 very short and band-like, closely united laterally; IBr_2 (ax) triangular, usually about twice as broad as long; IBr_1 and first two brachials in lateral contact, though not laterally flattened.

Ten arms; proximal brachials discoidal, or oblong, then becoming triangular, at first broader than long, later about as long as broad, and wedge-shaped terminally.

Oral pinnules longer than, but not quite so stout as, those succeeding; middle pinnules with more or less developed spinous edges and dorsal processes on the joints.

Distribution.—Caribbean Sea, northward to South Carolina and southward to Brazil.

Depth.—Sublittoral, and down to 262 fathoms.

5. LEPTONEMASTER, new genus.

Genotype.—*Leptonemaster venustus*, new species.

Description.—Centro-dorsal a thin flat disk; cirrus sockets in a single marginal row.

Cirri XV–XX, 12–15, long and slender; first joint short, second half again as broad as long to nearly square, third about twice as long as its terminal diameter, fourth the longest, two and one-half to three times as long as its proximal diameter, fifth a transition joint, not quite so long as the fourth, with a dark band about its center; following joints gradually decreasing in length, the antepenultimate being very slightly longer than broad, or squarish, and the

penultimate squarish or not quite so long as broad; second to sixth joints slender, moderately constricted centrally ("dice-box shaped"), with prominent articulations, rounded in cross-section, then becoming rather strongly compressed laterally (the distal portion of the cirrus therefore becoming broader in lateral view) and less and less "dice-box shaped;" transition and following joints with a small, though prominent, sharp subterminal dorsal spine; opposing spine slightly marked, median, arising from the entire dorsal surface of the penultimate joint; terminal claw somewhat longer than the penultimate joint (about as long as the antepenultimate), moderately stout, and moderately curved, the curvature being strongest in the basal portion.

Ends of the basal rays visible as rather prominent tubercles in the angles of the calyx; radials entirely hidden or slightly visible over the ends of the basal rays, separated distally; IBr_1 short, nearly four times as broad as long, the proximal edge convex, not in contact basally, rounded and widely free laterally, the sides of adjacent IBr_1 making with each other an angle of about 90° ; IBr_2 (ax) triangular, the anterior angle somewhat produced, about one and one-half times as broad as long, the very short lateral edges making an obtuse angle with those of the IBr_1 .

Ten arms; first seven brachials approximately oblong, then becoming obliquely wedge-shaped, and after the tenth triangular, about as long as broad, and terminally obliquely wedge-shaped and longer than broad, with somewhat expanded articulations; after about the sixth the brachials develop strongly produced and overlapping distal ends. Syzygies occur between the third and fourth brachials, again between the tenth and eleventh to twelfth and thirteenth, and distally at intervals of three oblique muscular articulations.

Disk naked; mouth and anal tube about equally eccentric.

P_1 the stoutest, and much the longest, evenly tapering to a flagellate tip; P_2 considerably shorter and much more slender than P_2 ; P_3 not much more than one-third, P_4 one-third the length of P_1 ; following pinnules increasing slowly in length, the distal being nearly as long as P_1 , with elongated joints which have expanded articulations, and spinous distal ends.

Distribution.—Caribbean coast of Central America, Gulf of Mexico, and northern coast of Cuba.

Depth.—Forty-two to 163 fathoms.

LEPTONEMASTER VENUSTUS, new species.

Centro-dorsal a thin flat disk, the small cirrus sockets arranged in a single crowded marginal row, usually five to each radial area.

Cirri XV–XX, 12–15 (most commonly 13 or 14) 10 mm. long, as described above.

IBr series and calyx elements as described.

Ten arms 70 mm. to 90 mm. long; first brachial short, slightly wedge-shaped, about three times as broad as the exterior length, entirely separated interiorly by the anterior apex of the IBr₂, the interior edges diverging at an angle of approximately 90° or slightly less; second brachial irregularly quadrate, slightly larger than the first; third and fourth brachials (syzygial pair) oblong, about half again as broad as long; next three brachials approximately oblong, about twice as broad as long, then becoming obliquely wedge-shaped, and after about the tenth triangular, about as long as broad, further out on the arm becoming very obliquely wedge-shaped (almost triangular) about as long as broad, and in the terminal portion longer than broad. After about the sixth the brachials develop strongly produced and overlapping distal ends.

P₁ 10 mm. long, with about thirty-five joints, moderately stout basally and evenly tapering; terminal comb with 13 to 15 teeth, preceded by two or three more or less rudimentary; teeth spade-shaped or triangular, longer than broad, slightly longer than the lateral diameter of the joint which bears them, well separated, and incurved; basal joints of the pinnule broader than long, the proportionate length gradually increasing, so that the joints from the middle onward are approximately squarish; the joints have prominent dorsal projections with the apex at the distal end, and strongly produced distal edges, these characters dying gradually away after about the middle of the pinnule; P₂ much more slender than P₁, 7 mm. long, the joints after the fifth squarish; first two joints with strong dorsal processes or broad carinations, that of the second the stronger; following joints with rounded dorsal processes and prominent distal edges; terminal comb rather long with sixteen fully developed and five or six smaller and more rounded teeth; teeth proportionately slightly longer and better developed than the teeth of P₁; P₃ about 4 mm. long, slender and delicate, the first two joints disproportionately large, about half again as broad as long, the second with a much produced distal dorsal angle or even distal half of the dorsal side; third joint squarish; following joints slightly longer than broad; third and following joints as far as the comb, as in P₂, with strongly produced coarsely spinous distal ends; comb as in P₂; P₄ 3.5 mm. long, slightly more delicate than P₃, with no enlargement of the two basal joints and no comb; first two joints short, third longer than broad, the following increasing slightly in length, being about half again as long as broad distally; third and following joints with produced and coarsely spinous distal edges; P₅ similar to P₄, 4 mm. long, with sixteen joints, but slightly stouter; following pinnules similar to P₅, increasing very gradually in length; distal pinnules 8 mm. to 9 mm. long, slender, with about 21 joints, the first two not so long as

broad, the third slightly longer than broad, the remainder becoming elongated and about three or four times as long as broad distally; third and following joints with expanded articulations and coarsely spinous distal ends.

Color (in spirits).—Brownish white, the perisome dark brown.

Type.—Cat. No. 25457, U.S.N.M., from *Grampus* station 5104, off the west coast of Florida; 51 fathoms.

6. COMISSIA, new genus.

1908. *Comaster* (part) A. H. CLARK, *Smiths. Miscell. Coll.* (Quarterly Issue), LII, p. 202.

Genotype.—*Comissia lütkeni*, new species.

Description.—Centro-dorsal discoidal, the bare polar area broad and flat, the cirrus sockets arranged in two closely crowded alternating rows.

Cirri XV–XXV, 16–24, resembling those of *Capillaster*; the fourth is a transition joint.

Ends of the basal rays visible as prominent tubercles in the angles of the calyx; radials very slightly visible over the ends of the basal rays, or quite concealed; IBr₁ short and broad, closely united laterally, more or less concealed by the centro-dorsal; IBr₂ (ax) triangular, about twice as broad as long, free laterally; synarthrial tubercles prominent.

Ten arms; first brachial short, slightly wedge-shaped, between three and four times as broad as long exteriorly, interiorly united; second brachial larger and much more obliquely wedge-shaped; third and fourth (syzygial pair) somewhat longer interiorly than exteriorly, about twice as broad as the interior length; following one or two brachials almost oblong, about three times as broad as long, then becoming triangular, about twice as broad as long, in the terminal part of the arm becoming very obliquely wedge-shaped, about as long as broad; brachials after the second with prominent and finely spinous distal ends and a very finely tubercular or spinous dorsal surface which in the terminal portion gradually become obsolete, so that the ends of the arms are practically smooth. Syzygies occur between the third and fourth brachials, again between the eleventh and twelfth to fourteenth and fifteenth, and distally at intervals of three oblique muscular articulations.

Disk naked, or with small scattered calcareous granules; mouth subcentral; anal tube small and marginal.

P₁ the longest; following pinnules decreasing gradually in length and slightly in stoutness to P₄, which is less than half as long as P₁, with somewhat less than half as many joints; following pinnules remaining similar for some time, then gradually becoming more slender and increasing in length to about the length of P₃ distally;

the joints of the middle and distal pinnules are slightly "dicebox-shaped," with a finely spinous surface and with the distal ends produced ventrally into two long sharp spines, one on each side of the perisome; this modification of the joints in the more proximal of the pinnules affects only the distal portion, but later encroaches more and more upon the proximal part, soon involving almost all of the joints.

COMISSIA LUTKENI, new species.

1908. *Comaster coppingeri* (part) A. H. CLARK, Smiths. Miscell. Coll. (Quarterly Issue), LII, p. 202 (ten-armed specimens).

Centro-dorsal discoidal, the bare polar area broad and flat, 4 mm. or 5 mm. in diameter; cirrus sockets arranged in two closely crowded alternating rows.

Cirri XV-XXV, 16-24 (usually 18-21) 7 mm. to 17 mm. long, comparatively small and rather stout; first joint over twice as broad as long, second and third nearly or quite as broad as long, fourth half again to nearly twice as long as broad, a transition joint, usually rather darker than the preceding, but light colored and with a polished surface in the distal fourth; following joints decreasing in length, after the eighth being about twice as broad as long; occasionally the fifth is a transition joint instead of the fourth, in which case the two are about of the same size: fourth and following joints with the dorsal and dorso-lateral distal edge everted and finely spinous; this eversion of the distal edge of the joints gradually narrows anteriorly, on the last two or three joints becoming merely a single blunt spine or tubercle; concurrently with its shortening, it gradually attains a crescentic form, so that in lateral view the joints from the fourth onward appear to be furnished with low dorsal spines which arise gradually from the whole dorsal surface, at first terminal, gradually becoming subterminal in position, and on the antepenultimate joint almost median: opposing spine median, arising from the entire dorsal surface of the penultimate joint, short and blunt, reaching not more than one-third the distal diameter of that joint in height; terminal claw about as long as the penultimate joint, stout, and moderately curved.

Post-radial elements as given in the generic description; the arms are 70 mm. to 75 mm. long.

P₁ 12 mm. to 15 mm. long, slightly stouter than the succeeding, though not especially large, with about thirty-five joints, at first about twice as broad as long, very gradually becoming longer and about as long as broad after the twelfth or fifteenth; terminal comb prominent, arising abruptly, with sixteen teeth, bluntly triangular, nearly twice as long as broad at the base, basally in apposition, about as high as the transverse diameter of the joints which bear them, rather strongly recurved; P₂ similar, 10 mm. to 12 mm. long; P₃

similar, 8 mm. to 10 mm. long; P_4 6 mm. long; P_5 and following pinnules 6 mm. long without combs, composed of sixteen joints, the first three not so long as broad, the remainder about as long as broad; distally the pinnules gradually increase in length and become more slender, being distally 8 mm. long with twenty-three to twenty-five joints, the first two short, the third and following longer than broad, becoming about twice as long as broad in the outer portion. The lower pinnules have the corners of the joints considerably cut away as in *Heliometra*; the joints of the middle and distal pinnules are slightly "dice-box shaped" with a finely spinous surface, and with the distal ends produced ventrally into two long, sharp spines, one on each side of the perisome; this modification of the joints in the more proximal of the middle pinnules affects only the distal portion, but later encroaches more and more upon the proximal part of the pinnules, soon involving almost all of the joints.

Color (in spirits).—Bright yellow, the skeleton lighter.

Type.—Cat. No. 25513, U.S.N.M., from *Albatross* station 5153; east of Port Dos Amigos, Tawi Tawi; 49 fathoms.

7. Genus CAPILLASTER A. H. Clark.

1758. *Asterias* (part) LINNÆUS, Syst. Nat., 10th ed., II, p. 663.

1772. *Asteria* (part) BRÜNNICH, Zoölogia fundamenta, p. 230 (emendation).

1816. *Comatula* (part) LAMARCK, Hist. nat. des animaux sans vertèbres, II, p. 530.

1836. *Comaster* (part) L. AGASSIZ, Mém. Soc. de sci. nat. de Neuchâtel, I, p. 193.

1841. *Actinometra* (part) J. MÜLLER, Archiv für Naturgesch., 1841, I, p. 140.

1849. *Comatula* (*Actinometra*) (part) J. MÜLLER, Abhandl. d. k. preuss. Akad., 1847, p. 246.

1849. *Comatula* (*Alecto*) (part) J. MÜLLER, Abhandl. d. k. preuss. Akad., 1847, p. 258.

1909. *Capillaster* A. H. CLARK, Proc. Biol. Soc. Washington, XXII, p. 87.

Genotype.—*Actinometra sentosa* P. H. Carpenter, 1888.

Distribution.—Madagascar to northern Australia, the Philippines, and Japan.

Depth.—Littoral and sub-littoral; rarely down to 160 fathoms.

8. NEMASTER, new genus.

1879. *Antedon* (part) RATHBUN, Trans. Conn. Acad. Sci., V, p. 157.

1880. *Actinometra* (part) P. H. CARPENTER, Journ. Linn. Soc. (Zool.), XV, p. 213.

1908. *Comaster* (part) A. H. CLARK, Proc. U. S. Nat. Mus., XXXIII, p. 685.

Genotype.—*Nemaster grandis*, new species.

Distribution.—Caribbean Sea and Atlantic coast of South America south to Bahia.

Depth.—Littoral, and down to 194 fathoms.

Diagnosis.—In general same as *Capillaster*; IIBr 4 (3+4); IIIBr 3 (2+3), or irregular; brachials at first oblong, then triangular, about as long as broad, wedge shaped and longer terminally; terminal comb usually repeated on inner side of proximal pinnules; side plates developed along the ambulacra.

NEMASTER GRANDIS, new species.

Centro-dorsal thick-discoidal, the polar area 5 mm. in diameter, deeply concave; cirrus sockets marginal, arranged in three closely crowded alternating rows.

Cirri XXV-XXX, 30-35, about 40 mm. long, large and stout; first joint short, about three times as broad as long; following joints gradually increasing in length to the sixth or eighth, which, with the three following, is squarish, then gradually decreasing, the joints from the twelfth or fifteenth onward being about twice as broad as long, but the last two are almost square again; a transition joint occurs between the seventh and the twelfth, proximal to which the joints have a dull, finely pitted surface, distally a highly polished surface, the pits widely scattered or absent, and dorsal projections; transition joint not especially marked; joints proximal to the transition joint with practically straight sides and no modification of the dorsal distal edge; transition and following joints with the distal dorsal edge projecting as a transverse ridge, coarsely dentate (usually tridentate), the ridge being equal in length (transversely) to about half the diameter of the joints; distally the ridge gradually narrows, becoming bidentate, and in the terminal four to seven joints resolves itself into a single spine, which on the antepenultimate becomes subterminal in position; all the transverse ridges appear as rather prominent spines in lateral view; opposing spine prominent, though short, rather stout, arising from the whole dorsal surface of the penultimate joint, about equal in length to one-third the diameter of that joint, the apex subterminal or submedian, the distal edge usually making much less of an angle with the transverse diameter of the joint than the proximal, giving the spine the appearance of leaning forward; terminal claw considerably longer than the penultimate joint, stout basally, slender distally, strongly curved proximally, but becoming nearly straight in the distal portion.

Ends of the basal rays visible as low tubercles in the angles of the calyx, but with difficulty differentiated from the adjacent parts; radials concealed in the median line, but visible as a rather prominent triangle in the angles of the calyx, the apex of which separates the lower corners of the IBr₁; IBr₁ oblong, rounded dorsally and laterally, about three times as broad as long, widely separated laterally; IBr₂ (ax) pentagonal, one-third to one-half again as broad as long, the

lateral edges diverging distally and about equal in length to those of the IBr₁; IIBr 4 (3+4); IIIBr 3 (2+3), the division series being separated by a distance about equal to the breadth of the IIBr series; if the full IIIBr series is not present, those on the exterior sides of the IBr series are most frequently absent, so that there is an approximation to a 1, 2, 2, 1 arrangement.

Twenty-four to thirty-one arms, about 200 mm. long; first brachial wedge-shaped, rather large, not quite half again as broad as the exterior length, almost entirely united interiorly; second and third brachials (syzygial pair) not quite so long as broad; next four brachials oblong, about twice as broad as long, then wedge-shaped, and after three or four triangular, about as long as broad; in the terminal portion of the arms the brachials become wedge-shaped, nearly or quite twice as long as broad. The distal edges of the brachials project slightly and are beset with fine spines. Syzygies occur between the second and third brachials, again between the fourteenth and fifteenth to twenty-second and twenty-third (usually in the vicinity of the eighteenth) and distally at intervals of three oblique muscular articulations.

Mouth marginal and radial; anus central; disk naked, about 30 mm. in diameter; side plates developed along the brachial and pinnule ambulacra.

P_D 30 mm. to 35 mm. long, stout, much stouter than the succeeding pinnules, but tapering evenly to a slender and flagellate tip, with forty to forty-five joints, all of which are approximately squarish; a slight prominence is visible on the dorsal side of the distal edge of the second joint, which rapidly becomes larger and increases in width on the succeeding joints, after about the seventh taking the form of a strong coarsely spinous eversion of the dorsal edge of the joints; this disappears near the proximal part of the distal comb; comb composed of fourteen teeth, arising abruptly; first tooth low and triangular; second oblong or slightly trapezoidal, usually slightly broader basally than high, the following becoming more obliquely trapezoidal and relatively somewhat higher, the terminal teeth being truncated-triangular; the more proximal teeth are not equal in height to more than three quarters of the lateral diameter of the joints which bear them, but the later teeth, owing to the distal tapering of the pinnule, become about equal to the lateral diameter; P_P about 25 mm. long, considerably less stout than P_D, but otherwise similar to it; P₁ about 20 mm. long, much less stout than P_P, similar to it; P₂ and following pinnules slender and delicate, about 10 mm. long; P₂ bears a comb distally, but the following pinnules are without combs; PP_{2, 3, 4}, and *a, b, c* have the first two joints disproportionately large and produced dorsally into large carinate processes; distal pinnules slender, about 12 mm. long, with about twenty-five

joints, the first over twice as broad as long, the second about as long as broad, the third longer than broad, the remainder about half again as long as broad. The distal ends of the joints are slightly everted and finely spinous; the dorsal surface is beset with fine spines, and the last four joints bear long recurved spines.

Type.—Cat. No. 25459, U.S.N.M., from *Albatross* station 2146; off Colon; 34 fathoms.

9. Genus COMATELLA A. H. Clark.

1874. *Actinometra* (part) LÜTKEN, Mus. Godeffr. Cat., V, p. 190.

1908. *Comaster* (part) A. H. CLARK, Proc. U. S. Nat. Mus., XXXIII, p. 685.

1908. *Phanogenia* (part) A. H. CLARK, Proc. U. S. Nat. Mus., XXXV, p. 124.

1908. *Comatella* A. H. CLARK, Smiths. Miscell. Coll. (Quarterly Issue), LII, p. 207.

Genotype.—*Actinometra nigra* P. H. Carpenter, 1888.

Distribution.—Ceylon to Fiji, Tonga, Samoa, and Japan; West Indies, St. Paul's Rocks, Atlantic coasts of southern Europe and northwestern Africa.

Depth.—In the Indian and Pacific oceans, littoral, and down to 140 fathoms; in the Atlantic 73–830 fathoms.

10. Genus COMASTER L. Agassiz.

1816. *Comatula* (part) LAMARCK, Hist. nat. des animaux sans vertèbres, II, p. 530.

1836. *Comaster* L. AGASSIZ, Mém. Soc. de Sci. nat. de Neuchâtel, I, p. 193.

1841. *Alecto* (part) J. MÜLLER, Archiv für Naturgesch., 1841, I, p. 147.

1849. *Comatula* (part) J. MÜLLER, Abhandl. d. k. preuss. Akad., 1847, p. 262.

1866. *Phanogenia* LOVÉN, Öfversigt k. Vetensk.-Akad. Förhandl., 1866, No. 9, p. 231.

1879. *Actinometra* (part) P. H. CARPENTER, Proc. Roy. Soc., XXVIII, p. 386.

Genotype.—*Comatula multiradiata* Lamarck, 1816 (not *Asterias multiradiata* Linnaeus) = *Alecto multifida* J. Müller, 1841.^a

Distribution.—Northern Australia to Luzon and the Mergui Archipelago.

Depth.—Littoral and sublittoral.

11. Genus COMANTHUS A. H. Clark.

1816. *Comatula* (part) LAMARCK, Hist. nat. des animaux sans vertèbres, II, p. 530.

1841. *Actinometra* (part) J. MÜLLER, Archiv für Naturgesch., 1841, I, p. 140.

1841. *Comaster* (part) J. MÜLLER, Archiv für Naturgesch., 1841, I, p. 140.

1841. *Alecto* (part) J. MÜLLER, Archiv für Naturgesch., 1841, I, p. 144.

1849. *Comatula* (*Actinometra*) (part) J. MÜLLER, Abhandl. d. k. preuss. Akad., 1847, p. 256.

^a Cf. Proc. Biol. Soc. Washington, XXII, p. 87.

1849. *Comatula (Alecto)* (part) J. MÜLLER, Abhandl. d. k. preuss. Akad., 1847, p. 260.

1891. *Goldfussia* (not of de Castelneau, 1843) NORMAN, Ann. and Mag. Nat. Hist., [6] VII, p. 387.

1908. *Phanogenia* (part) A. H. CLARK, Proc. U. S. Nat. Mus., XXXV, p. 124.

1908. *Comanthus* A. H. CLARK, Proc. Biol. Soc., Washington, XXI, p. 220.

Genotype.—*Comanthus intricata* A. H. Clark, 1908.

Distribution.—South Africa westward and northwestward, along the southern coast of Asia and the entire coast of Australia, throughout the East Indies, to southern Japan, the Kingsmill (Gilbert) Islands, Fiji, and Samoa.^a

Depth.—Littoral and sublittoral.

^a Carpenter records *C. rotalaria* ("*Actinometra parvicirra*") from Peru, in South America, and others have since accepted this record. This Peru is, however, undoubtedly Peru or Francis Island, situated approximately in lat. 1° 30' S., long. 176° 00' E., in the Gilbert group, north of Fiji.

A NEW SQUIRREL FROM DIRECTION ISLAND, SOUTH CHINA SEA.

By MARCUS WARD LYON, JR.,

Second Assistant Curator, Division of Mammals, U. S. National Museum.

On his way to Borneo, in 1907, Dr. W. L. Abbott stopped for a day at Direction Island, where he secured a single specimen of the new species of plantain squirrel described below. Direction Island, also called Pulo Mankotan and Pulo Pengiki Kichil (or Paneeky Ketchil), lies in the South China Sea in latitude $0^{\circ} 14' 39''$ north and longitude $108^{\circ} 1' 53''$ east. Politically and geographically it is a member of the Tambelan group, of which it is the most southeastern. An account of the mammals of this group and of some adjacent islands was published by Mr. Gerrit S. Miller, jr.,^a in 1900.

Doctor Abbott says of the island: "It is about three-fourths mile long by about one-fourth mile wide, and 500 to 600 feet high. The surface is rocky, but covered with trees except at the southwest corner, where a clearing has been made by the Orang Laut, who occasionally visit the island. Here a few cocoanuts have been planted, also some bananas and papaya. A number of squirrels were heard, but only two were seen, of which one was shot. No other mammal was seen, although there were doubtless rats. There were many white fruit pigeons. Turtles had been laying their eggs on the sand beach, where there were also many tracks of *Varanus* lizards."

SCIURUS DIRECTOR, new species.

Type.—Skin and skull of an immature (large permanent upper premolar just displacing the milk tooth) male, Cat. No. 145392, U.S.N.M., collected on Direction Island, South China Sea, May 1, 1907, by Dr. W. L. Abbott. Original number, 5152.

Diagnostic characters.—A "red"-bellied member of the *vittatus* group characterized by a more ruddy cast to the entire pelage than usual.

^a Mammals collected by Dr. W. L. Abbott on islands in the South China Sea, Proc. Wash. Acad. Sci., II, pp. 203-246, August 20, 1900.

Color.—Upper parts of head and body, a fine grizzle of black and ochraceous or ochraceous-buff, both colors about equally mixed, the ochraceous being somewhat paler over the shoulders than elsewhere, and darkest posteriorly and in the region of the thighs; upper surface of the tail very similar to upper surface of head and body in color, but the grizzling is coarser and in certain lights the tail appears finely annulated; outer sides of thighs and arms similar to back, but with finer grizzling and the ochraceous predominating; upper surfaces of feet dull ochraceous darkened by the blackish bases of the hairs showing through; light side-stripe, about 55 by 5 mm., between buff and ochraceous-buff; dark side-stripe, about 50 by 7 mm., blackish finely sprinkled with ochraceous-buff; underparts and inner side of fore and hind legs a color something between Ridgway's ochraceous-buff and ochraceous-rufous; underside of tail a very coarse grizzle of blackish and ochraceous, the latter color predominating in the middle line; inner side of ears and an orbital ring, the lower half of which is most pronounced, ochraceous-buff; outer side of ears similar to adjacent parts of head; cheeks and base of whiskers similar to rest of head, but grizzle very fine and the ochraceous-buff predominating.

Skull and teeth.—These show no special peculiarities; the audital bullæ and teeth, however, are smaller than they are in the majority of species of squirrels of the *vittatus* group.

Measurements.—External measurements taken by collector: Head and body, 190 mm.; tail vertebræ, 182; hind foot, with claws, 49. Cranial measurements: Greatest length, 46.4; basal length, 39; zygomatic breadth, 26.7; interorbital constriction, 16; mandible, front of symphysis to back of condyle, 29.5; maxillary toothrow (alveoli), 9.2; mandibular toothrow (alveoli), 8.7.

Specimens examined.—One, the type.

Remarks.—Compared with its geographical neighbor, *Sciurus abbottii* Miller,^a of Big Tambelan Island, *S. director* is conspicuously more ruddy throughout, being ochraceous or ochraceous-rufous where *S. abbottii* is only buffy or ochraceous-buff. Among the forms of the *S. vittatus* group of squirrels in the National Museum *S. tedongus* Lyon,^b from the island of Banka, most nearly resembles *S. director*, but is less ruddy, except on the belly, which has about the same color in the two species.

^a Proc. Wash. Acad. Sci., II, p. 224, August 20, 1900.

^b Proc. U. S. Nat. Mus., XXXI, p. 591, December 18, 1906.

THE THORAX OF INSECTS AND THE ARTICULATION OF THE WINGS.

By ROBERT EVANS SNODGRASS,

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I. INTRODUCTION.

This paper is an attempt to show the unity of thoracic structure that prevails throughout all the orders of insects. It is hoped that it will be of special service to systematists in entomology and that it will meet with approval from students of morphology. The material on which the paper is based was all drawn from the U. S. National Museum and the dissections have been deposited in the museum.

The work has been done under the direction of Dr. A. D. Hopkins, of the U. S. Bureau of Entomology, and has grown from an attempt to determine thoracic homologies in the Coleoptera, especially in the family Scolytidae. It is published by the approval of Dr. L. O. Howard, chief of the bureau, as a contribution from the office of Forest Insect Investigations. The author is indebted to Doctor Hopkins not only for the opportunity of carrying on the work but also for a great deal of help in doing it and for the verification of observations. Assistance has also been received from other members of the entomological staff of the bureau, among whom are Mr. Nathan Banks, Mr. A. N. Caudell, Mr. D. W. Coquillett, Mr. R. P. Currie, Dr. H. G. Dyar, Mr. Otto Heidemann, Mr. E. A. Schwarz, and Mr. H. S. Barber and also Mr. J. C. Crawford, of the U. S. National Museum.

Some of the drawings on the plates were used by the writer in a former paper on the thorax, published in the Proceedings of the Washington Entomological Society (1908), and are here reproduced with the permission of the editors of that journal.

No new theory is presented. The writer claims that the diagrams forming text figures 1 to 6 represent simply the facts. All schemes of thoracic symmetry in consecutive circles are discarded on the ground that they are supported only by the imagination.

The following statements sum up the principal conclusions: (1) There is no reason for believing that the parts of any thoracic segment are derived from more than one metamere, though the primitive thoracic region may have been composed of more than three segments, remnants of the supernumerary ones being possibly represented by the intercalary plates of some of the Aptera; (2) the thoracic sclerites are subdivisions of an original undivided segmental wall; (3) the sclerites of the pleurum are homologous throughout all the orders and modifications are brought about principally through the coalescence of the pleurites; (4) the tergum consists of a primitive undivided notal plate carrying the wings and, in the adult meso- and metathorax of all the principal orders, except the Orthoptera, of a second postnotal or pseudonotal plate developed in the membrane behind the first and having no connection with the wings; (5) the divisions of the notum are secondary, though similar in most of the orders, and are not necessarily homologous, while modifications are brought about through a stronger subdivision into distinct regions and even into separate sclerites.

It is unfortunate for modern entomology that there are so many species of insects. Entomologists early had to specialize as Coleopterists, Dipterists, Lepidopterists, and so in each order a scheme of anatomy and a nomenclature grew up which satisfied the needs of the worker in that order but had no necessary connection with those of workers in other groups. It is true that Andouin in 1824 worked out a system of comparative external anatomy and proposed a universal set of names for the sclerites. It is true also that his names have been in large part employed by nearly all subsequent entomologists. But in the actual application of Andouin's names to the sclerites of the thorax, specialists in the various orders have differed widely on account of their ignorance concerning the correspondence of parts in different insects. Recent entomologists who have attempted to enforce a uniformity of nomenclature based on a more thorough knowledge of insect structure are confronted with the nonconforming masses of literature which must form the basis of work by present and future students in each order. However, even if systematists never can employ a uniform system of names, it can not be denied that it is best to know the true homology of the parts as far as this can be determined.

It is impossible to follow the rule of priority in selecting anatomical terms, for the name must be descriptive of the part to which it is applied. The earlier entomologists also paid little attention to the duplication of parts in successive segments, but gave a separate name to every piece. Andouin did away with this system in 1824 and firmly established a nomenclature based on the belief that each thoracic segment is a modification of one plan of structure. He

should be taken as the Linnaeus of thoracic nomenclature, and there is not sufficient reason on any ground for applying new terms to the parts he named.

In the study of the wings the venation nomenclature established by Comstock has been adopted. No attempt has been made to prove or to disprove Comstock's interpretations of the veins in the main part of the wing. While a study of the basal structure may show definitely that some particular vein is absent as a distinct trunk at the base, it still remains an open question whether this vein is actually gone or is fused with the one before or behind it. The general venation must furnish the evidence in most such cases.

II. THE SEGMENTATION OF THE HEAD AND BODY.

A few decades ago an insect was defined as a creature consisting of a head, a thorax subdivided into three segments, and an abdomen composed of 10 or 11 segments. Such a definition, however, would not satisfy the demands of most present-day entomologists, and it is interesting to contemplate the shock some antievolutionary forefather of entomology would receive could he now see in print the statement that an insect is composed of 40 segments. This said forefather might be in some measure pacified, however, were he to learn that the insects themselves have not been required to keep pace with the ideas of entomologists concerning them.

1. SEGMENTATION OF THE HEAD.

If the question as to how many embryonic metameres form the head of an insect could be decided by a vote among present and past students of the subject, the six-segment theory would undoubtedly be established. The problem of head segmentation has been attacked from both an anatomical and an embryological standpoint, but, since the embryologists attempt to discover the actual facts of development, it would seem that deference should be paid to their opinions. Furthermore, the embryologists agree more closely among themselves than do the anatomists. Although the number of head metameres claimed by the former varies from four to seven, this discrepancy is not what it appears to be in figures, for the chief point of disagreement is whether the three preoral segments apparent in the embryo are actual metameres or are only secondary divisions. The real question is thus reduced to one between six and seven segments.

On the other hand, the anatomists describe from four to nine segments without any alleviating circumstances. The number of theories seems to agree closely with the number of theorizers. Comparative anatomy as a key to morphology has been so thoroughly deposed in vertebrate craniology that we must regard it with great suspicion in

entomology. On the other hand, its advocates may, of course, point out that adult insects are so specialized that even the embryo in many respects does not repeat phylogeny. Yet it has never been shown that the head is a case in point. It certainly at an early embryonic stage consists of a series of segments and no evidence has been offered to prove that these embryonic segments are not true metameres.

The principal anatomists who have mapped out the head on purely anatomical grounds are Newport (1839), Janet (1899, 1900), and Verhoeff (1905). Newport went at the subject in the simplest manner possible. He virtually drew circles around the head corresponding with the plates of the dorsal surface, namely, (1) the labrum, (2) the clypeus, (3) the front (clypeus posterior), (4) the small sclerites sometimes found about the bases of the antennæ, and (5) the epicranium. He thus had five segments which were composed laterally and ventrally by whatever fell between two of the inclosing lines.

Later anatomists have not been satisfied with this direct and simple arrangement by Newport. Janet (1899, 1900) makes out nine head segments which he arranges in three sets of three each and then points out the nice conformity in which the set of three thoracic segments follows. He does not even intimate, however, by what natural law the head should be a multiple of the thorax, or why his theory should be more plausible by making it such.

Verhoeff (1905) discredits embryology as a guide in the study of the morphology of the insect head, and, on purely anatomical grounds, elaborates a scheme of eight segments for the head of the Dermaptera. The labrum, the clypeus, and the front, according to his plan, are the first three terga, while the sterna of these segments form the epipharyngeal membrane and the anterior part of the throat. These segments constitute the "protocephalon." Following them are an antennal segment (a preantennal segment being absent in Dermaptera), and a premandibular segment, constituting the "deutocephalon." Finally, the three jaw segments form the "tritocephalon." The mentum and submentum form the sterna of the labial and maxillary segments, respectively. This view assumes that the maxillæ originate *behind* the labial palpi. In the Chilopoda the so-called maxillæ are much more like the ligula and labial palpi of insects than like the insect maxillæ, while the chilopod labium consists principally of the leg-like palpi, thus suggesting that the hexapod first maxillæ are the chilopod second maxillæ. If this should be true, then the theory advanced by Banks (1893) that the poison fangs have coalesced with the second maxillæ in Chilopoda to form the first maxillæ of Hexapoda appears more possible. Otherwise, Banks had to assume that the poison claws moved forward past the bases of the second maxillæ and then fused with the first maxillæ. A combina-

tion of the poison claws and the labial palpi of the chilopods would form an organ much more nearly resembling the insect maxillæ than would a union between the poison claws and the first maxillæ of chilopods.

All reasoning of this fascinating sort, however, simply shows the limitless extent to which morphological theorizing can be carried on anatomical grounds.

Verhoeff's theory of head segmentation has been severely criticised by Heymons (1905) on the ground that the facts of embryology utterly refute it, and that it does not conform with the segmentation of the nervous system.

The simplest embryological view holds that there are four segments in the head—a preoral, a mandibular, a maxillary, and a labial segment. This is advocated by Lowne (1892), who regards the three embryonic divisions of the preoral region as secondary. Bengtsson (1897, 1905) adopts this view concerning the preoral region, but he finds four segments in the postoral part of the head. Almost all students of the embryology of the insect head, however, regard the three preoral divisions as true metameres. Hence, embryologists are divided in opinion mainly between six and seven head segments. The principal advocates of six segments are Zaddach (1854), Huxley (1878), Viallenes (1887), Wheeler (1893), Heymons (1895), Packard (1898), Riley (1904), and Holmgren (1904, 1907). The advocates of seven head segments are Folsom (1899, 1900) and Comstock and Kochi (1902). But these authors are supported also by Bengtsson (1897, 1905) and by Börner (1904) in so far as they find four postoral segments, though they recognize only one preoral segment.

The seven-segment theory is based mainly on Folsom's (1900) observation that seven pairs of ganglia appear in the head soon after involution, and that in *Anurida maritima* a pair of appendages or "superlinguæ" appear back of the mandibles, corresponding with the fourth pair of ganglia. These appendages fuse in most insects with the lingua of the embryo to form the hypopharynx of the adult, but in many lower forms they remain as the lateral lobes of the hypopharynx or "endolabium" and have been misleadingly called the "paraglossæ." Börner (1904) finds that the hypopharynx of nearly all insects having incomplete metamorphosis is a compound structure formed of the median "glossa" and the lateral paired elements, which he calls the "maxillulæ." (The reader must remember that the terms "glossa" and "paraglossæ" have been inconsiderately applied by some recent entomologists to the parts of the hypopharynx or "endolabium," while they properly belong to the outer or true labium.) Börner thus recognizes four postoral segments. Hansen (1893) suggested that the "paraglossæ" (superlinguæ, maxillulæ) of

Machilis are homologous with the first maxillæ of Crustacea, and Folsom concurs in this view. Apparently no one has compared them with the paragnatha of Crustacea.

Holmgren (1907), on the other hand, claims that these superlingual processes arise from the premandibular segment and are innervated from the tritocerebrum. It would seem that he must refer to a different pair of appendages, namely, the second antennal rudiments or "intercalary appendages." His observations were made on a fly larva (*Phalacroccra*).

Bengtsson (1897, 1905), however, describes an endolabium in *Phalacroccra* which includes "paraglossæ," equivalent to the superlinguæ of lower insects. Holmgren (1907) refutes this idea entirely, and claims that Bengtsson's so-called endolabium of fly larvæ is not the endolabium of lower insects but simply the terminal lobes of the ordinary outer labium, of which Bengtsson's "ectolabium" is the mentum and submentum. He furthermore asserts that what Bengtsson takes for nerves going to this endolabium from the superlingual ganglion are simply muscle fibers, though Bengtsson (1905) had stoutly defended his former observations (1897).

The best summarized statement of the segmentation of the head is that made by Comstock and Kochi (1902). Although some work has been done since, but little new information has been added. The preoral part of the head consists of three embryonic segments corresponding with the three lobes of the brain, namely, the protocerebrum, the deutocerebrum and the tritocerebrum. The first segment has no appendages, but it innervates the eyes; the second is the antennal segment; the third carries the "intercalary appendages"—vestigial organs observed by many embryologists in the Aptera (Wheeler 1893, Uzel 1897, Claypole 1898, Folsom 1900), possibly in the Diptera (Holmgren 1907), and in the Hymenoptera (Bütschli 1870). These rudimentary appendages correspond with the second antennæ of Crustacea.

The postoral region of the head and the mouth parts are certainly derived from at least three embryonic segments, or, according to many embryologists, from four. The first is the mandibular segment. The possible second is the one under dispute, but so many embryologists have described two small appendages back of the mandibles which fuse with the median lingua to form the hypopharynx that their existence can not be doubted, and it is reasonable to suppose they represent a segment. Riley (1904), however, shows that these superlingual appendages, or maxillulæ, are absent in the embryo of *Blatta*, and he doubts that they are actual appendages where observed. Berlese (1906) also does not recognize a superlingual segment. Following this doubtful metamere is the segment of the first maxillæ, and finally that of the second maxillæ or labium.

Comstock and Kochi (1902) attempt to assign the various head sclerites of the adult to individual segments of the embryonic head. Riley (1904) in studying the cockroach arrives at different results, but he discredits the reliability of all attempts to map out the adult head according to segments. In discussing Comstock's view, he says: "My results have convinced me that so intimate a relation between primary segmentation and the sclerites can not be shown."

Of course, the ventral part of the preoral region becomes dorsal so that the mouth, which is originally on the middle of the ventral surface of the head, comes to be situated anteriorly. Thus the labrum, clypeus, and front are developed from a primitive ventral surface. So, in a general way, the other sclerites arise from definite regions, but they are simply secondary divisions of a continuous head capsule, and the notion that they are modified terga, pleura, and sterna of the head metameres appears to be entirely unsupported by actual evidence.

The last head segment is the one that chiefly concerns us in a study of the thorax. All embryologists seem to agree that its body forms the sclerites found in the neck of the adult and that only its fused appendages, the labium, become associated with the head, except when there is a gular plate present, which sclerite is derived from its sternum. This embryonic segment can, therefore, hardly be spoken of as a head metamere. It is the segment of the neck and this, in the adult, has received the name of "microthorax."

Hence we would accept six primitive head segments, providing the apparent superlingual segment is a real one, and one microthoracic or neck segment.

2. SEGMENTATION OF THE BODY.

The foregoing discussion of the segmentation of the head has been made more extensive, perhaps, than a mere introduction to the study of the thorax would require. But the writer wishes to illustrate to anyone not familiar with the subject the utter futility of attempting a study of metamerism on an anatomical basis. The embryology of the thorax has never brought out much more than that three segments compose it, except in the Hymenoptera, where the first abdominal segment is fused with the thorax. Hence there are no embryological facts concerning the thorax by which anatomists can be held in check, but, with the unfortunate example of both the vertebrate and the insect head in mind, one must certainly regard with much doubt all theories of thoracic metamerism based on a study of the plates forming the very apparent three segments in the adult. Riley (1904) makes the following appropriate statement:

It would seem that the definitive sclerites can afford little or no evidence as to the primary segmentation of insects. This is certainly true of the head sclerites

and I see no reason why it should not apply to other regions of the body. Sclerites originate from mechanical causes and do not necessarily have any relation to the primary segmentation.

Lowne (1892) in discussing the prevalent notion of the dual structure of the thoracic segments states that he does not admit it proved, and does not see that it helps in the understanding of the morphology of the insect segment.

The writer, then, wishes to say emphatically that he discards everything but plain statements of the facts in the description of the thorax. Since, however, modifications of the same plan of thoracic structure recur throughout the insect orders, this fact can be taken as evidence that all the sclerites, especially those of the pleurum, have not been produced independently in the different orders.

Many writers have supposed that each thoracic segment consists of two united segments. The arrangement of the plates on any typical segment would suggest this—the dividing line on the side passing between the episternum and the epimerum, on the back between the scutum and scutellum, and on the venter between the sternum and sternellum. Some authors have adduced further evidence of the dual nature of the segment from the apparent division of the coxa in some orders into an anterior and a posterior part.

Banks (1893), arguing from the coalescence of segments in the Chilopoda, concluded that the thorax of insects is formed of five segments, the first, third, and fifth retaining the legs, the second and fourth bearing the wings. He regards the coxæ as double and cites the meso- and metacoxal appendages of *Machilis* as examples of remnants of the ventral appendages of segments two and four. He points out that in *Scutigera* (the highest chilopod) the small terga, after the first segment, are united with the larger ones so that the first segment bears only one pair of legs while the following bear two pairs each. It is only a step from this to suppose that in *Machilis* the second leg of each pair has become rudimentary, forming the coxal appendages, while the first of each pair has persisted as the functional walking appendage. Banks does not seem to regard the cervical sclerites of insects as representing a segment in the thoracic series.

Patten (1890) gave other reasons for regarding each segment as double, adduced from a study of the mouth parts and the nerves.

Walton (1900) still further supports this theory by a study of the coxæ. He concludes that in both the Chilopoda and the Hexapoda the coxa is composed of an anterior part, "coxa genuina," and a posterior part, "coxa meron." These two coxal segments falling in line with the episternum and epimerum, and the arrangement of the thoracic muscles, form his basis for believing the entire segment a compound of two primitive segments.

Now, it is only in the mesothorax and metathorax of Mecoptera Neuroptera, Trichoptera, and Lepidoptera that the coxa is actually a double structure. In these orders the coxa genuina of Walton carries the trochanter, while the coxa meron is attached to the coxa genuina only. In other orders in which the coxa shows a more or less evident division this division is in the coxa genuina itself, the coxa meron being absent, and is of the nature of a strengthening of the coxa by opposite ridges on its inner walls. In the Neuroptera and Trichoptera at least it can easily be demonstrated, by a study of larval and pupal forms, that the "coxa meron" is simply a detached extension of the epimerum, which fuses upon the posterior side of the true coxa. It is, hence, not a part of the primitive coxa at all, and the apparent double coxa in these orders is a purely secondary condition. (See special descriptions under Neuroptera, p. 564, and Trichoptera, p. 565, also p. 542 and figs. 144-148.)

Comstock and Kochi (1902) show that the plates of each segment may be arranged into two subsegments, but defer any opinion as to whether they represent two primitive segments or not.

It will be found that all these theories are purely imaginative. Embryologists have not shown that the plates of any thoracic segment are derived from more than one metamere. However, it may be true that two, three, or four segments primarily existed where there is but one in insects as we now know them. Verhoeff (1902, 1903, 1903a, 1903c, 1904, 1904a) is the principal elaborator of this theory.

Verhoeff bases his ideas on a study of the Aptera, the Embiidæ, and the Dermaptera, and especially on a comparison of *Japyx* with the Chilopoda. He first points out the tendency in the Chilopoda toward the suppression of every alternate segment by a fusion with the preceding larger spiracle-bearing segment. In *Japyx* there are remnants of extra segments between the pro- and mesothorax, and between the meso- and metathorax, represented principally by well-developed tergal and sternal plates. Thus the thorax would consist of six segments in three pairs, namely, the microthorax and prothorax, the stenothorax and mesothorax, and the cryptothorax and metathorax. Verhoeff observes, however, that this arrangement does not correspond with that of the Chilopoda, because the small segment in *Japyx* is associated with the large segment following instead of with the one preceding. Then, as if to remedy this discrepancy, he further discovers traces of still other thoracic segments, one between the stenothorax and the mesothorax and another between the cryptothorax and the metathorax. Finally, by the aid of small presternal plates ("vorplatten") he is able to construct the following table of complete uniformity in segmentation between Scolopendridæ and Japygidæ (Verhoeff, 1904a):

SCOLOPENDRIDÆ.

Head.
 Maxilliped segment.
 First leg-bearing segment.
 Intercalary segment.
 Second leg-bearing segment.
 Intercalary segment.
 Third leg-bearing segment.
 Intercalary segment.
 Fourth leg-bearing segment.
 Intercalary segment.
 Fifth leg-bearing segment.
 Intercalary segment.

JAPYGIIDÆ.

Head.
 Microthorax.
 Prothorax.
 Presternal plates (vorplatten).
 Stenothorax.
 Small intercalary ring.
 Mesothorax.
 Presternal plates (vorplatten).
 Cryptothorax.
 Small intercalary ring.
 Metathorax.
 Presternal plates (vorplatten).

Thus, it is supposed that *two pairs* of Scolopendrid segments—a leg-bearing and an intercalary segment in each pair—have been reduced to *one segment* in ordinary insects. This reduction has resulted not from a combination of segments but from a suppression first of the intercalary segments of the chilopod and then of the alternate remaining leg segments. The intercalary segments of Scolopendridæ, in other words, are not the small segments of *Japyx*, but are the much more rudimentary traces of segments between these and the large segments. Verhoeff's own statement (1903c) is as follows:

The intermediate segments (zwischen-segmente) of insects are reduced primary segments, inherited from Chilopodan ancestors and which have united into a double segment with the large primary segment immediately behind, while the intercalary segment of the original double segment of the Chilopods has become almost entirely extinct.

According to this theory, then, the primitive thorax consisted of ten segments. However, all but three of these have been eliminated in all but the very lowest insects, and the eliminated segments have taken no part in the formation of the plates of the body wall in present-day insects. It is certainly no difficult matter to show that the sclerites are formed during postembryonic growth and are purely secondary divisions of the body wall of one segment. Hence, this theory of Verhoeff's is entirely tenable, since it deals only with conditions which are presumed to be obliterated before the thoracic plates begin to form.

However, it must be admitted that all this elaborate scheme is based on an excessive use of the imagination. No proof is adduced to show that the intermediate and intercalary sclerites of *Japyx* are not secondarily developed plates or even subdivisions of the principal segments. Desguin (1908), in reviewing this notion of the multiple nature of the thorax in Aptera, concludes that neither the anatomical nor the embryological evidence is sufficient to prove whether these intermediate sclerites represent true segments or not. Börner (1903) also gives a good criticism of some of Verhoeff's extravagant theories.

Verhoeff extends his view of the many-segmented structure of the insect body to the abdomen (1903a, 1903c, 1904). Here he finds, in the region of the first seven ordinary segments, seven primary segments and seven secondary ones. Beyond these are two genital segments, then the segment carrying the cerci, and finally, in the lowest insects, traces of three more beyond the last—the pygidium, the metapygidium, and the telson. The gonapophyses and the cerci are carried by the fifteenth, sixteenth, and seventeenth primitive segments, which are the eighth, ninth, and tenth persisting segments. Verhoeff thus makes out a total of twenty abdominal segments. Add to these the ten thoracic segments, one microthoracic segment, and nine head segments, and an insect assumes the dignity of a creature of forty segments!

III. THE MICROTHORAX.

Embryologists have shown that the sclerites of the neck, the second maxillæ of the head, the hind part of the subœsophageal ganglion, and the gular plate, when present, are all derived from one metamere. They usually reckon this metamere as the last segment of the head, while anatomists call its cervical parts in the adult the *microthorax*. This term has become pretty well established and will be adopted in the present paper, but not implying that it is a part of the true thorax. On the other hand there is no reason for calling it a head segment. In many of the lower insects its appendages, the second maxillæ or labium, are not attached to the head but are suspended from the gular membrane and associated much more closely with the microthoracic sclerites than with the head (*Spodromantis*, 25, *Sm.*). The fact that the microthoracic ganglion is fused with the true head ganglia preceding it signifies nothing more than does the fusion of the first abdominal ganglion with that of the metathorax. It is only when the sternal plate becomes transferred to the ventral surface of the head, as the gula, that the microthorax takes any part in the actual formation of the head.

Verhoeff (1902) regards the segment of the maxillipeds or poison claws in the Chilopoda as the equivalent of the microthorax in insects. This, however, is denied by Silvestri (1902), who says that the maxilliped segment of the Chilopoda is the prothorax of insects. Verhoeff (1903b) then further shows that in *Scolopendra* there are four pairs of nerves going to this segment, of which the second is the largest and innervates the appendages. In *Polyspilota striata*, a Mantid, he discovers the same four pairs of nerves arising from the subœsophageal ganglion back of the labial nerves and going to the microthorax and salivary glands. Here, however, the second is the weakest and obviously because there are, according to Verhoeff's view, no microthoracic appendages, the labium not being regarded as such.

There is evidently a lack of harmony here unless it be that the first maxillæ of the Chilopoda correspond with the superlinguæ of the Insecta, the second maxillæ with the maxillæ, and the poison claws with the labium. In this case we could regard the microthorax of insects as the maxilliped segment of the Chilopods, which, from superficial appearances, would not seem impossible.

The sclerites of the microthorax are well known. They have been studied extensively by Verhoeff (1902) and occur in nearly all the orders of insects. They are specially well developed in the Odonata (5, 6, 7, 8, 9, 12, *Mi* and 1 *mi*, 2 *mi*, 3 *mi*, 4 *mi*), in the Orthoptera (24, 25, 36, 37, 45), and in the Euplexoptera (93), but occur in a more reduced condition in many of the other orders, such as the Coleoptera (95, *Mi*) and the Diptera (174, *mi*, *mi*). In the Orthoptera and Euplexoptera they often form an almost complete segment presenting tergal, pleural, and sternal plates. Verhoeff has gone so far as to identify all the pleurites of a thoracic segment in the microthorax, but undoubtedly this is establishing homologies on a too imaginative basis. Comstock and Kochi (1902) regard the gular sclerites of the head as the microthoracic sternum, and in some of the Euplexoptera (93) the microthoracic sternites are so large and so associated with the head as to suggest the gular sclerite of the Coleoptera.

We may conclude that there is no reason for regarding the microthorax as anything more than the neck segment whose sclerites are reduced to the small neck sclerites and the gular plate when the latter is present, whose ganglion has fused with the last head ganglion, and whose fused appendages become attached to the head in most cases and constitute the labium. It should not be included, in reckonings of the number of segments forming the head, as one of the head segments. (See note on page 595.)

IV. THE THORAX.

In a former paper (1908) the writer gave a brief account of the structure of the insect thorax. This description can now be amplified by illustrations taken from all the principal orders. For convenience the subject will be divided under three heads, namely, (1) the tergum, (2) the pleurum and coxa, and (3) the sternum.

1. THE TERGUM.

The word *tergum* is here used to designate all the chitinized parts of the dorsum of any segment. It is generally used interchangeably with the term "notum," but where the tergum consists of two plates the latter name, *notum*, will be restricted in this paper to the first or wing-bearing sclerite, and the term *postnotum* or *pseudonotum* (Verhoeff, 1903) applied to the posterior or post-alary plate. The notum is the plate which, by diversities of its surface topography,

becomes divided into the more or less definite regions usually called the *prescutum*, *scutum*, and *scutellum*, while the postnotum remains undivided and is the *postscutellum*. The postnotum does not occur in the Orthoptera; it does not occur in the nymphs of any insects, even though well developed in the adults; it does not occur in the pupæ of Neuroptera and Coleoptera at least; and it is never present in the prothorax. Therefore it is most probably not a primitive tergal plate, and the term *pseudonotum* fits it very well. Verhoeff (1903) gave this name to the postnotal plate of the Euplexoptera (Dermaptera), though he may not have intended its general use in the sense here applied.

Text figures 1 and 2 diagrammatically represent the relation of the notum (*N*) and the pseudonotum (*PN*) to each other and to the wing, the last being carried entirely by the notum. Fig. 3, representing a segment in side view, shows the pseudonotum continuous laterally with the epimerum (*Epm*). This is the most frequent condition, though often there is a line between the two and sometimes they are only articulated or merely contiguous.

This figure and figure 2, giving a ventral view of the tergum, both show the postphragma (*Pph*) depending from the posterior edge of the pseudonotum, though it is often restricted to the middle of the latter.

The pseudonotum always carries the postphragma. Verhoeff regards it as a development of the postphragma, but it is probably a better statement of the facts to say that the phragma is a development of the pseudonotum, for in the lower insects the latter is a large flat plate, while the phragma may be simply a thin fold projecting downward from its posterior edge. In the mesothorax of Lepidoptera, Hymenoptera, and Diptera this condition, however, is reversed, the phragma being developed to a great size, although the pseudonotum itself is not reduced. The postphragma is really a

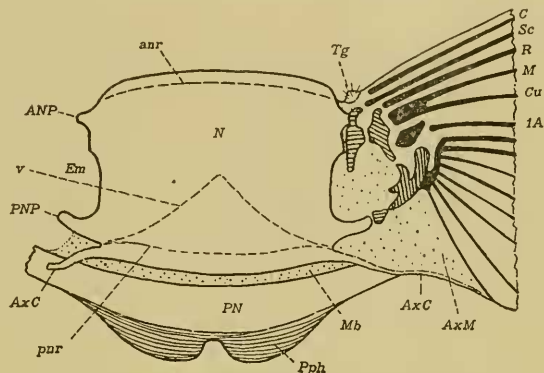


FIG. 1.—DIAGRAMMATIC TERGUM OF ANY COMPLETE WING-BEARING SEGMENT, AND THE BASE OF THE WING, DORSAL VIEW; 1A, FIRST ANAL VEIN; ANP, ANTERIOR NOTAL WING PROCESS; *anr*, LINE OF ANTERIOR VENTRAL NOTAL RIDGE (ANR OF FIG. 2); *AxC*, AXILLARY CORD; *AxM*, AXILLARY MEMBRANE; *C*, COSTA; *Cu*, CUBITUS; *Em*, LATERAL EMARGINATION OF NOTUM; *M*, MEDIA; *Mb*, MEMBRANE BETWEEN NOTUM AND PSEUDONOTUM; *N*, NOTUM; *PN*, PSEUDONOTUM OR POSTNOTUM; *PNP*, POSTERIOR NOTAL WING PROCESS; *pnr*, LINE OF POSTERIOR VENTRAL NOTAL RIDGE (PNR OF FIG. 2); *Pph*, POSTPHRAGMA; *R*, RADIUS; *Sc*, SUBCOSTA; *Tg*, TEGULA; *v*, LINE OF MEDIAN OR V-SHAPED VENTRAL NOTAL RIDGE (*V* OF FIG. 2).

chitinization of the infolded intersegmental membrane behind the pseudonotum, for it is always composed of two closely appressed or fused laminae. The first is directly continuous with the pseudonotum, the second is connected with the notum of the segment following, generally by membrane but sometimes directly, as when the segments are fused.

The pseudonotum is conspicuous in the metathorax of Coleoptera (132-140, *PV*). It is the plate that Straus-Dürckheim (1828) named the "tergum" in *Melolontha vulgaris* (135, *PV*), but most authors have followed Audouin (1824) and Newport (1839) in calling it the "postscutellum." This name is appropriate when a scutum

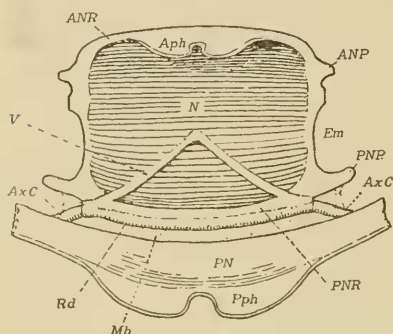


FIG. 2.—DIAGRAMMATIC TERGUM OF ANY COMPLETE WING-BEARING SEGMENT. VENTRAL VIEW; ANP, ANTERIOR NOTAL WING PROCESS; ANR, ANTERIOR NOTAL RIDGE; Aph, PREPHRAGMA; Ax C, AXILLARY CORD; Em, LATERAL EMARGINATION OF THE NOTUM; Mb, MEMBRANE BETWEEN NOTUM AND PSEUDONOTUM; N, NOTUM; PV, PSEUDONOTUM; PNP, POSTERIOR NOTAL WING PROCESS; PNR, POSTERIOR NOTAL RIDGE; Pph, POSTPHRAGMA; Rd, POSTERIOR REDUPLICATION OF THE NOTUM; V, V-SHAPED VENTRAL RIDGE OF NOTUM, THE ENTODORSUM.

and scutellum can be distinguished. Berlese (1906) recognizes and figures the plate in the Coleoptera, but he refers it to the abdomen, calling it the "acrotergite" of the first abdominal segment. Such a disposition of the sclerite, however, is clearly impossible on account of its intimate connection, an articulation (*i*) in beetles, with the epimera of the metathorax. In the mesothorax of Coleoptera there is no pseudonotum unless the two small plates (127, 128, 131, *q*) yoking the mesonotum to metanotum are rudiments of it. The pupae of beetles do not show a pseudonotum even in the metathorax. In *Dendroctonus valens* (122, 126), and in *Tetropium velutinum* (123) it is easy to see

that no pupal plate intervenes between the metathoracic notum or wing-bearing sclerite (*N₃*) and the first abdominal tergum (*IT*). The latter can be identified by the first abdominal spiracles.

In the Plecoptera the pseudonotum is a large, simple plate in both the meso- (75) and the metatergum. It is partly overlapped by the notum (*N*). In a nymphal tergum, however, there is no trace of it (76), and its site is entirely membranous (*Mb*). It is similar in Neuropteran adults (142), but lacking in the pupa (141).

In the Lepidoptera (149), the Hymenoptera (169), and the Diptera (174 and 179) the pseudonotum is present in both segments and is easily distinguishable as the tergal plate behind the wing bases. In the mesothorax of these orders it carries the large phragma (150,

163, 170, 179, *Pph* or *Pph*₂) that projects posteriorly through the metathorax and almost shuts off the cavity of the thorax from that of the abdomen. In a Tipulid pupa (173) the mesopseudonotum (*PN*) is present as a large plate intervening between the two wing-bearing plates (*N*₂ and *N*₃). It is interesting to note here that the halter is a wing-like structure (*W*₂).

The pseudonotum has been discussed at considerable length because the fact has apparently not been recognized by other authors that the postscutellum or pseudonotum is an independent plate in its origin and is, hence, not one of the divisions of the notum, as is the prescutum, scutum, or scutellum.

The notum (*N*) or wing-bearing plate of a meso- or metathoracic tergum is diagrammatically illustrated in figs. 1, 2, and 3. In its simplest form it is an undivided plate, convex dorsally. On its ventral surface (fig. 2) the anterior and posterior margins are thickened, forming the anterior notal ridge (*ANR*) and the posterior notal ridge (*PNR*). The latter is generally folded forward a short distance on the ventral surface, forming a free posterior reduplication (*Rd*) which often overlaps the sclerite following. The lateral margins of the notum are produced into two processes which carry two of the articular sclerites of the wing base. These lobes are the *anterior notal wing process* (*ANP*) and the *posterior notal wing process* (*PNP*). The posterior edge of the notum, formed by the posterior reduplication, usually appears as a marginal thickening which is continued outward on each side as a corrugated, cord-like thickening of the anal edge of the basal membrane of the wing. These thickenings may appropriately be called the *axillary cords* (*AxC*). They are important characters in determining the posterior limit of the notum. The anterior notal ridge bears the *anterior phragma* or *prephragma* (*Apk*).

This outline might be taken to represent the structure of the meso- or metatergum of primitive winged insects, for it is approximately that of nymphal and some pupal forms though these lack the notal wing processes. A pseudonotum is never present in nymphal stages and the prephragma is usually but little developed. The tergum of the nymph is illustrated in the Odonata (15), in the Mantidæ (31), in the Acridiidae (56, 58) and in the Perlidae (76). The same simplicity is exhibited by the pupal tergum of Coleoptera (122, 123, 126). In a Tipulid pupa (173), however, the pseudonotum is present in the mesothorax as a distinct plate (*PN*₂) between the two wing-bearing plates (*N*₂ and *N*₃). As will be shown later, the notum of the adult is commonly divided more or less distinctly into several regions or even sclerites. But a study of nymphs and pupæ shows conclusively that these notal divisions are secondary characters in the growth of the individual. The tergum consists at

first of one plate—the notum, from the entire lateral margins of which the wings develop. Behind the notum is added, in the adult stage, the pseudonotum (postscutellum) as a distinct plate, while the so-called prescutum, scutum, and scutellum are formed as secondary divisions of the notum. These notal regions, moreover, are not homologous in all the orders. This can be proved by a study of the ventral surface of the notum, which presents certain fundamental characters common to nearly all insects. Two of these are the anterior and posterior notal ridges (fig. 2, *ANR*, *PNR*) already described; a third, and the most important one, is the V-shaped ridge (*V*), the *entodorsum* of Amans (1885), located on the posterior half of the notum, having its apex forward and the bases of its arms fused with the posterior ridge. A comparison of text figs. 1 and 2 will show that the three ventral ridges (*ANR*, *V*, *PNR*) form three transverse lines on the surface of the notum (*anr*, *v*, *pnr*).

These ridges and their surface lines are undoubtedly homologous structures in all insects. They mark off the area of the notum into four regions, as follows: (1) A narrow anterior marginal band in front of the line of the anterior ridge; (2) a large bilobed region situated between the line of the anterior ridge (*anr*) and that of the entodorsum (*v*) and carrying the notal wing processes (*ANP*, *PNP*); (3) a triangular space between the line of the entodorsum and that of the posterior notal ridge; and (4) a narrow posterior marginal band terminating laterally in the axillary cords (*AxC*) and forming the posterior free edge or reduplication of the notum.

This typical simplicity of structure is illustrated in the Orthoptera by *Blattella* (38, 40) and *Gryllus* (49, 50), and in the Neuroptera by *Corydalid* (142, 143). It will be observed that the pseudonotum (*PN*) is absent in the Orthoptera, but well developed in *Corydalid*.

These four regions of the Orthopteran notum are very suggestive of the four divisions of the tergum as ordinarily recognized, but a comparison with *Corydalid* (142) at once shows that the term "postscutellum" can not be applied to any part of the Orthopteran tergum, for the name belongs to the pseudonotum, which is absent in Orthoptera. Hence, all identifications of a "postscutellum" in Orthoptera, supposed to be homologous with that of the higher orders, are erroneous. A comparative study of the orders shows that the posterior line (*pnr*) is generally absent, that the notum is very commonly divided by lines or actual sutures into three subdivisions, and that these lines or sutures are *not* determined by the ventral ridges and do not bear the same relation to them in the different orders.

Thus we have the following premises: (1) The ventral ridges of the notum are constant in all the orders and are, hence, fundamental homologous structures; (2) three notal divisions are of general

occurrence but are not constant nor do they present the same relation to the ventral ridges in the different orders. From these facts it follows that the notal divisions are not necessarily homologous wherever they occur, though they may be so within limited series, and that they are simply secondary adaptations to some common demand upon the notum.

The above statements and conclusion can be verified by a study of the species illustrated on the plates. Since the subdivisions of the notum are best developed in the highest orders these will be described first. The ordinary names of *prescutum* (*pse*), *scutum* (*set*), and *scutellum* (*scl*) will be used to designate the notal regions, but the reader must bear in mind that they are not used in the different orders in a homologous sense, and that the abbreviations on the figures do not designate parts necessarily homologous. The "postscutellum" will be called the pseudonotum (*PV*).

The notal divisions are probably as well shown in the mesothorax of a Tipulid fly as in any other insect. In *Holorusia grandis* (174, 175) the prescutum (*pse*) is a large plate with its posterior margin produced posteriorly in a large V-shaped angle, having no relation to the anterior notal ridge. The lateral posterior angles are produced into two small lobes (175, *u*) lying opposite the anterior angles of the wing bases. The scutum (*set*) is a wide plate carrying the anterior notal wing processes (*ANP*). The scutellum (*scl*) consists of a median elevated shield and of a depressed area on each side. The posterior wing processes belong to the latter, though they are separated from it by a tongue of membrane. The ventral V ridge is present just as in the diagram (fig. 2), but it marks only the apex (*v*) of the scutellum, its lateral parts not showing on the surface. Thus the three divisions of the Tipulid notum are but slightly influenced by the ventral ridges. The pseudonotum (*PV*) is well developed, consisting of a median and two lateral plates, the latter articulated with the epimera (174, *Epm*). In a Tabanid (179, 180) the third division of the notum (*scl*) is distinct but the first (*pse*) and the second (*set*) are not separated mesially. The lateral angles (*u*) of the prescutum, as in *Holorusia*, lie opposite the wing bases.

In the Hymenoptera similar divisions of the notum occur, as is well shown in the drawing (160) of *Parasiobla*, a Tenthredinid. An examination of the ventral surface reveals the V ridge present but situated entirely behind the suture between the scutum and scutellum. These two plates, furthermore, are easily separable along this suture and, hence, the latter can in no way be compared with the dividing line between the scutum and scutellum of the Orthoptera. In the example given (160) the prescutum (*pse*) is perfectly exposed, but it is more commonly hidden in the Hymenopteran mesothorax by the pronotum (169, *N*₁), which is attached to and overlaps

the anterior part of the mesothorax. The pseudonotum (*PN*) is also usually hidden on account of its projecting downward before the metathorax. It can easily be shown, however, by removing the mesotergum from the surrounding parts (163, 170).

The metanotum in both the Diptera and Hymenoptera is reduced in size and the subdivisions are not well marked (174, 169). The metapseudonotum is present in both orders but is generally very narrow in the Diptera. In the Hymenoptera it is usually a large plate (160, 169, *PN*₃) continuously fused on the sides with the metaepimera (*Epm*₃), though in some cases it is narrow and scarcely distinguishable from the metanotum (164).

In the Hymenoptera there occurs a fusion of the first abdominal segment with the metathorax. This fact has led to a great deal of discussion among entomologists and to the production of an immense amount of literature. Latreille (1821) first described the rear part of the apparent Hymenopteran thorax as being a part of the abdomen and named it the "segment médiaire." Newman later (1833) called it the "propodeon." Packard (1866), by a study of the development of *Bombus*, proved that the first abdominal segment is actually transferred to and becomes consolidated with the metathorax. A great many other writers have written a great many opinions about it and about the opinions of other writers, and Goseh (1881) has furnished a voluminous historical account of all the opinions of all these writers up to his time. To his Contribution to the History of Entomology (1881) the reader is referred if he is interested in this phase of the subject. If not, the examination of a few specimens of the insects concerned will probably suffice.

The abdomen of *Cimbex* (166) shows clearly enough that the first abdominal segment (164, *IT*) is much more closely attached to the thorax than to the rest of the abdomen. That the part in question is the first abdominal segment is proved by its spiracles (*I Sp*) and by the structure of the metathorax and of the rest of the abdomen. The metathorax of *Cimbex* (164) has, in addition to the attached part (*IT*), its full complement of sclerites. The notum (*N*) and pseudonotum (*PN*) are present dorsally and the episternum (*Eps*) and the epimerum (*Epm*) laterally. In the abdomen itself, if the first segment behind the one in question is counted as the first, there would be present only nine segments in all, and the absurdity would be forced upon us of referring the female gonapophyses to the seventh and eighth segments. Hence, arguing from either end, the conclusion would be that the *median segment* belongs to the abdomen. In *Parasitobla* (160) this segment could never be regarded as more than a slightly transposed part of the abdomen. However, in the higher forms, of which *Pepsis* (169) is a good representative, the median segment is so intimately grown into the metathorax that it certainly does not

appear to belong to the abdomen. Yet in the metathorax there is present the true metathoracic notum (N_3), and the pseudonotum (PV_3) identifiable by its fusion with the metathoracic pleura. Hence the large corrugated plate (IT) behind the pseudonotum has no place in the metathoracic anatomy, and its abdominal origin is proved by its spiracles (ISp). Thus a study of comparative anatomy proves conclusively that the "segment médiaire" is at least the first abdominal tergum which has been transferred to the thorax, and *Pepsis* indicates that the entire first abdominal segment is so transferred. If this is true, then the ventral part disappears as a distinct plate in the higher families.

In the Lepidoptera the mesonotum has much the same appearance as in the Diptera and Hymenoptera, but differs in details of structure. In the Cossidae (149, 150) it consists of a large scutum (*set*) and scutellum (*scl*) separated along the line of the ventral V-ridge, and of a very narrow prescutum (150, *pse*). The postscutellum (*PV*) is present, but normally (149) is almost hidden between the mesothorax and the metathorax. In the Sphingidae (155, 156) the prescutum depends vertically from the anterior edge of the scutum (155) and carries the prephragma (*Aph*). The prescutum in *Phassus* is, therefore, much more nearly the equivalent of the anterior division of the notum in the diagram (fig. 1) than in either the Hymenoptera or the Diptera and, hence, is more similar to the Orthoptera (38) and Neuroptera (142). In the Diptera, it will be recalled, the prescutum is large and extends back to the bases of the wings. In the Hymenoptera it is remote from the wing bases. In *Phassus* (150) the scutum carries both the anterior and the posterior-wing processes of the notum, while in *Protoparce* (156) the posterior processes arise from the scutellum. This is due to the fact that here the lateral parts of the scutellum are not defined by the ventral V-ridge, but appear simply as depressed areas at the sides of the median elevated part of the scutellum as in *Holorusia* (175) and *Tabanus* (180). In this case the separation between the scutum and scutellum laterally is simply a matter of topography.

The metathorax of *Phassus* (149, 151) is larger and more like the mesothorax than is usual among the higher insects. The prescutum (*pse*) and the scutellum (*scl*) almost meet on the median line, thus separating the scutum into two lateral plates (*set*). The posterior wing processes (*PVP*) arise in the angles between the scutellum and the scutum.

The scutellum in all the forms so far described carries the axillary cords of the wings (*AxC*) at its extremities. These cords, which are distinct in nearly all insects, are, hence, diagnostic of the location of the scutellum in Lepidoptera, Hymenoptera, and Diptera, defining its posterior margin, and consequently, the posterior edge of the

notum. The postscutellum (*PN*) lying behind them is always a plate more or less distinctly separated from the notum, but connected or continuously fused with the epimera.

In the Coleoptera there occur two special modifications of the metathoracic tergum which set the beetles apart in this respect from all the other orders. One of these characters is the forward extension of a median tongue of the scutellum toward the prescutum, cutting the scutum into separated lateral halves. The second character is the division of each lateral scutal plate again into two by lines formed by special transverse ventral ridges laterad of the apex of the V-ridge.

In a separate paper (1909) the author has shown that Audouin's interpretation of the coleopteran tergum is untenable, that, in order to make out his four transverse tergal sclerites, Audouin has represented certain parts as continuous which in nature are separate, and in other cases has made separations where none occur.

A Carabid, *Calosoma scrutator* (132, 133), presents a very simple arrangement of the metatergal subdivisions characteristic of the beetles. The prescutum (*psc*) consists of a large quadrate median part and of two narrow lateral arms widened terminally into the triangular anterior notal wing processes (*ANP*). The median part is separated by a membranous area (*mb*), the "toile" of Straus-Dürckheim (1828), from the anterior extension of the scutellum on the floor of the median notal groove (*G*). On its anterior ventral edge the prescutum carries the prephragma (*Aph*) mesially and the cup-shaped muscle apodemes (*MD*) laterally. The scutum (*set*, *set*) is divided into four plates by the median approximation of the prescutum and scutellum, and by the lines (132, *w*) formed by the special transverse ventral ridges (133, *w*). The posterior division on each side carries the posterior notal wing process (*PNP*). The scutellum (132, *sel*) presents a median enlargement carrying the tongue extending forward on the floor of the median notal groove (*G*) and determined by the entodorsum or ventral V-shaped ridge (133, *V*), while laterally it extends to the bases of the axillary cords (*Ax C*) as a narrow marginal postscutal strip on each side, determined by the posterior notal ridge (*PNR*).

Behind the notum, and entirely separated from it by a flexible suture, is the pseudonotum (postscutellum) (*PN*), carrying the postphragma (*Pph*) and articulating at its extremities (*i*) with the epimera.

Dytiscus dauricus (136, 137), is very similar in its metatergal structure to *Calosoma* (132, 133). The lateral arms of the scutellum, however, are larger and, in addition to carrying the axillary cords, they support the combined bases (*r*) of the anal veins of the wing. The ventral ridges (137, *V*, *w*) are much larger than in *Calosoma*.

The higher families of beetles, illustrated by *Hydrophilus triangularis* (134), *Melolontha vulgaris* (135, 138), and *Cyllene robiniae* (140), have a prescutum somewhat different in appearance from that of *Calosoma* and *Dytiscus*. In *Hydrophilus* (134) and *Cyllene* (140) its median part (*pse*) is narrow and arched forward, and the membranous area (*mb*) back of it is extended transversely. The scutellum (*sc*) appears to have a long median tongue (*G*) by itself entirely separating the scutum into lateral halves. The anterior scutal subdivisions, in front of the transverse dividing lines (*w*), which are incomplete in *Hydrophilus*, are reduced to turgid antero-lateral corner lobes. The lateral extensions of the scutellum in each of these genera fuse laterally with the parts in front of them, so that the axillary cords (*AxC*) appear to be attached to the margins of the scutum (134, 140). *Melolontha vulgaris* departs still more widely from the *Calosoma-Dytiscus* type. The median part of the prescutum is represented entirely by the very large prephragma (135, 138, *Aph*), which is supported by the lateral parts of the prescutum and separated from the scutum and scutellum by an extensive membranous area (*mb*). The scutum (135, *sc*, *sc*) is divided, as in the other genera, into lateral halves by a median tongue of the scutellum (*sc*) on the floor of the median notal groove (*G*), but the transverse ridges (138 *w*) are coincident with the anterior scutal margins and do not subdivide the scutal plates. The scutellum (*sc*) is not defined laterally, but two triangular postero-lateral divisions of the scutum, the "scapulaire posterieure" of Straus-Durekheim (1828) carry the posterior notal processes (*PNP*) and the axillary cords.

The pseudonotum is well developed in all of these genera (134, 135, 140, *PN*) and carries the postphragma (*Pph*). The latter is specially large and of complicated structure in *Melolontha* (139, *Pph*).

The mesonotum of beetles is apparently constructed on the same plan as the metanotum. A pseudonotum is lacking. In *Calosoma* (127) and *Dytiscus* (128) the prominent shield-shaped area (*sc*) corresponds with the median part of the scutellum of the metanotum, lateral arms extending from it which carry the axillary cords (*AxC*). Laterad of the median shield are the separated halves of the scutum (*sc*) carrying the posterior wing processes of the notum (*PNP*). In front of it is a large complex prescutal part (*pse*) carrying the anterior phragma (*Aph*) and laterally the anterior notal wing processes (*ANP*). Two little plates (*q*) lie between the mesonotum and the metanotum. These may be rudiments of a mesopseudonotum, but they are more closely connected with the metanotum than with the mesonotum. On the ventral surface of the mesonotum (131) a V-shaped ridge (*V*) is present similar to that of the metanotum. In most other beetles the parts of the mesonotum are so blended that any plan of structure closely corresponding with that of the metanotum

can not be made out. Yet a progressive modification from the *Calosoma-Dytiscus* type can be traced through *Hydrophilus* (125), *Cyllene* (129), and *Dendroctonus* (124).

It is thus clear that the same fundamental structure of the notum obtains throughout the Coleoptera, the Lepidoptera, the Hymenoptera, and the Diptera, but that the notal subdivisions are not necessarily determined by it.

In the Neuroptera a tergum of diagrammatic simplicity is found. In *Corydalis* (142, 143) the scutum (*sc*) and scutellum (*sc*l) are separated along the line (142 *c*) of the ventral V ridge (143 *V*). Anteriorly and posteriorly are narrow marginal areas defined by the anterior and posterior notal ridges (*ANR*, *PNR*). The first of these might be called the prescutum, but the second is simply the posterior notal reduplication (*Rd*) and does not correspond with the postscutellum of higher orders, for this is the pseudonotum, which is well developed in *Corydalis* (142, *PV*).

In the Euplexoptera the metanotum of *Spongiphora* (96) consists of an undivided plate carrying both the anterior and the posterior wing process (*ANP*, *PNP*), while articulated near the middle of its posterior margin are two long arms (*f*) bearing the axillary cords (*AxC*). In the mesonotum (90) there is a large anterior triangular part carrying the anterior notal wing processes (*ANP*) and two lateral divisions carrying the posterior wing processes (*PNP*). It is evident, however, that neither tergum of *Spongiphora* is normal, for neither presents any trace of the V-shaped ridge, and the general shape is peculiar to the order. A ventral view of the mesonotum (92) shows that the two apparent divisions are due merely to elevations and depressions of the surface.

In the Belostomidae of the Hemiptera the mesonotum presents a wide, strongly declivous prescutal area carrying the prephragma and limited posteriorly by a definite transverse line. Back of it are two transverse grooves separating three other divisions. The last is simply the long posterior reduplication which in the Hemiptera overlaps the mesonotum. There is but a faint trace of the V ridge in *Benacus* and it does not influence the notal subdivision. The metanotum is also much modified, carrying an unusually large prephragma and lacking the V ridge. In *Benacus* (87) it is clear that both of the notal wing processes (*ANP* and *PNP*) arise from the scutum. A very narrow pseudonotum (88 *PN*) is present, connecting with the epimera laterally. The first abdominal tergum (*IT*) is also much modified and closely connected with the pseudonotum. It can be identified by its lateral spiracles (*I Sp.*).

In the Plecoptera, as illustrated by *Pteronarcys californica* (75), the indistinct regions of the notum are due entirely to the topography. The anterior and posterior notal regions are weakly developed while

there are but indistinct traces of the V ridge. The apex of the latter is entirely lacking, so that the area corresponding with the median part of the scutellum of the Diptera or Lepidoptera here appears as a median posterior lobe of the scutal region. This is very suggestive of the Acridiidae. The pseudonotum (*PN*) is a large plate equally developed in both meso- and metathorax of adults, though conspicuously absent in the nymphs.

The simple type of tergum occurring in the Orthoptera has already been described and is illustrated by *Blatella* (38, 40) and by *Gryllus* (49, 50). Both of these forms present a meso- and metanotum of almost typical diagrammatic form. The pseudonotum is lacking in all Orthoptera (see p. 558), and the divisions of the notum are only such as are indicated by the ventral ridges. All other regional diversifications are purely topographical.

In a winged Locustid, *Microcentrum laurifolium*, neither the mesonotum (39) nor the metanotum (41) shows any subdivisions except such as are marked out by elevations and depressions. Only rudiments of the V ridge occur (*V*). A small-winged adult Locustid, such as *Anabrus simplex*, has the notum (42) of almost nymphal simplicity.

In the Acridiidae the meso- and metanotum are almost identical with each other. An under view of the mesonotum of *Hippiscus phoenicopterus* (54) shows considerable departure from the other Orthopteran families. The V-shaped ridge (*V*) is low and flat and not ridge-like. The posterior notal ridge (*PVR*) is, however, well developed and is almost phragma-like. Diverging forward and outward from its middle are two high thin ridges (*s, s*) which do not occur in the other families. The posterior reduplication (*Rd*) forms a marginal thickening carrying laterally the axillary cords (*AxC*). On the dorsal surface (53) five regions are distinguishable. The first is a narrow median anterior area separated by a suture-like line (*anr*) formed by the anterior notal ridge. The second occupies most of the back and consists of two large anterior lateral lobes and of a smaller median posterior lobe. It bears the anterior notal wing processes (*ANP*). The third and fourth divisions lie laterad of the median posterior lobe and are demarked by the lines of the posterior notal ridge (*pnr*) and the ridges (*s, s*) diverging from the latter. Each is a transverse, elongate oval area tapering mesially, laterally bearing the posterior wing process (*PNP*). The fifth region, marked in front by the line of the posterior notal ridge (*pnr*), is the thickened posterior reduplication carrying the axillary cords (*AxC*).

This description, as far as the writer can see, expresses the facts concerning the Acridiid mesonotum. Yet, various entomologists, by a vigorous exercise of the imagination, have made out four transverse divisions, thus compelling the locust to fall in line with the beetles,

moths, and flies. It may be very gratifying to imagine that it does, but, when it clearly does not, what is gained by imagining that it is as it is not?

The pronotum of nearly all the Orthoptera is a simple plate, but when we come to the Acridiidae we find it divided into four very distinct transverse parts. In fact the pronotum of *Melanoplus* affords the most popular illustration of the quadruple construction of the insect back. But here (51) it must be observed that the notum not only covers the dorsum, but has usurped the territory of the pleurites (*Eps*, *Epm*) which it has all but crowded out. An examination of the inner surface (52) shows that the third external groove (*z*) marks an internal ridge against which the inner lamina of the long posterior reduplication (*Rd*) ends. The middle groove (*y*) marks a large internal notal ridge (*NR*) exactly similar to the internal pleural ridge (*PR*) of any normal thoracic pleurum such as that of the mesothorax of *Anabrus* (44) or of *Dissosteira* (71). There is present even a notal apodemal arm (*NA*) representative of the normal pleural arm (*PA*). The coxa is carried by an apparently notal coxal process (*NCxP*) in every way similar to the ordinary pleural coxal process (*CxP*), though this may really belong to the rudimentary pleurum. Finally, the leg muscles are disposed upon the notal surfaces at each side of the middle notal ridge just as they are upon the episternum and epimerum of a normal pleurum. Hence, it is clear that we have here simply a secondary modification of the notum due to its assumption of the duties of the pleural plates which it has crowded out. It is really most illogical that the pronotum of *Melanoplus* should be offered as a typical example of a thoracic tergum, for a tergum doing duty as both notum and pleura is, on the face of it, not typical. Yet in almost any discussion of insect anatomy the prescutum, scutum, scutellum, and postscutellum will be found principally illustrated by the pronotum of an Acridiid.

In the Odonata the pronotum of both nymphal and adult forms is divided into three transverse lobes by two transverse grooves. They are best developed in adults (5, 7, 9, 13), but are well marked also in the nymphs (8, 12). An unusual feature in some is the extension downward from the third lobe of a postepimeral strip (*a*) of the notum. The meso- and metanotum are sufficiently shown by the illustration of *Pachydiplax longipennis* (17). The two are similar and each is subdivided somewhat as in the Acridiidae and the Perlidae. The wing articulation shows few of the characters common to all the other orders except the Ephemera, and the wing muscles are nearly all attached to the base of the wing itself, a condition peculiar to the order. The pseudonotum (*PN*) is well developed in each segment. In the mesothorax (*PN₂*) it is exceptionally large and is divided by ventral ridges into a median and two lateral lobes.

The Ephemerid mesotergum and metatergum are sufficiently shown in the drawings of *Hexagenia bilineata* (4, 3). Each presents simply a confusion of elevations and depressions showing little similarity to any other order. A posterior median lobe, however, suggests the similarly situated lobe in Odonata (17), Acridiidae (53), and Perlidae (75), and also the median part of the scutellum of Lepidoptera (150), of Hymenoptera (161), and of Diptera (175). It is also comparable with the median shield-shaped area of the mesothorax of Coleoptera (127, 128). A pseudonotum (3, *PV*) is present in each segment, but is hidden from above by a posterior membranous fold margined by the axillary cords (4, *Ax C*).

This review of the notal structure in the different orders will show that the diagrammatic conception of the notum illustrated in fig. 2 is really the fundamental notal structure that prevails in all the principal orders except the Ephemerida and the Odonata. It is evident that the three ventral ridges—the anterior, the V-shaped, and the posterior—are constant characters and that the regions they mark off can be regarded as homologous in all the orders. But such subdivisions are not the ones usually apparent on the surface, and the latter, though generally the same within an order, vary so much in different orders that they can not be regarded as homologous structures except within limited series.

Three factors contribute to the formation of the notal subdivisions as follows: (1) Topography, as elevations and depressions of the surface forming more or less distinct regions, some of which appear variously modified throughout nearly the entire insect series; (2) ventral ridges, three of which are constant characters and, hence, to be regarded as homologous in the different orders; and (3) depressed suture-like lines and actual sutures, variable and not the same in different orders and, hence, not necessarily defining homologous sclerites.

Therefore, it may be concluded from a study of development and comparative anatomy that any scheme of thoracic structure in insects is untenable which postulates four primitive transverse plates in the tergum. Much less is there any evidence that the definitive tergum is composed of the united terga of two or four primitive metameres.

This conclusion is opposed to that of Berlese (1906), who finds in the thoracic terga of all orders four exactly corresponding parts, the "acrotergite," the "protergite," the "mesotergite," and the "metatergite." An examination of his colored diagrams (1906, Plate 4) will show, however, that in order to carry out his scheme Berlese has in many cases drawn purely arbitrary lines across the notum. Moreover, he has disposed of the pseudonotum by making it the "acrotergite" of the segment following the one to which it is attached. Thus he equates the mesopseudonotum and its phragma in *Sphinx* with the metaprephragma of *Acridium*. The pseudonotum

(postscutellum) of *Hydrophilus* he evidently calls the acrotergite of the first abdominal segment and equates it with the anterior subdivision of the first abdominal tergum of *Aceridium*. He appears to disregard entirely the intimate connections of the pseudonotum with the epimeral plates belonging to the segment of the preceding notum and its attachment to the preceding notum itself.

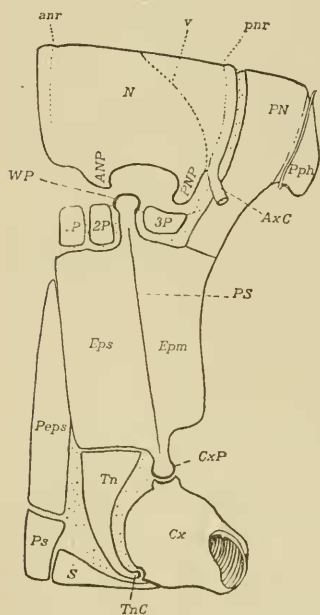


FIG. 3.—DIAGRAMMATIC LATERAL VIEW OF ANY COMPLETE WING-BEARING SEGMENT, EXTERNAL; ANP, ANTERIOR NOTAL WING PROCESS; anr, LINE OF ANTERIOR VENTRAL NOTAL RIDGE; AxC, AXILLARY CORD; Cx, COXA; CxP, COXAL PROCESS OF PLEURUM; Epm, EPIMERUM; Eps, EPISTERNUM; N, NOTUM; 1P, 2P, EPISTERNAL PARAPTERA OR PREPARAPTERA; 3P, EPIMERAL PARAPTERUM OR POSTPARAPTERUM; PN, PSEUDONOTUM OR POSTNOTUM; PNP, POSTERIOR NOTAL WING PROCESS; pnr, LINE OF POSTERIOR VENTRAL NOTAL RIDGE; Pph, POSTPHRAGMA; PS, PLEURAL SUTURE; Ps, PRESTERNUM; S, STERNUM; Tn, TROCHANTIN; TnC, TROCHANTINAL COXAL CONDYLE; v, LINE OF VENTRAL V-SHAPED NOTAL RIDGE; WP, PLEURAL WING PROCESS.

2. THE PLEURUM AND COXA.

The key to the structure of the pleurum is the *pleural suture*. To determine this proceed as follows: Find the pleural process that supports the base of the wing; locate the pleural condyle to which the coxa is articulated; observe the impressed line that extends between these two articular knobs. This is the pleural suture. The *episternum* lies in front of it, the *epimerum* behind it. In wingless forms the pleural suture must be determined by the coxal articulation alone. The suture may be horizontal, in which case the contiguous plates necessarily lie above and below it. Very rarely it is lacking, though such is conspicuously the case in the metathorax of most of the Hymenoptera. Internally the pleural suture forms a large ridge along its entire length, and this *pleural ridge* is of great assistance in determining the pleural suture when the latter is obscure or when there are other similar sutures externally.

The plan of any wing-bearing thoracic pleurum is illustrated diagrammatically by figs. 3 and 4. Externally (fig. 3) is seen the *pleural suture* (PS) extending upward to an arm bearing the wing, the *pleural wing process* (WP) and ventrally to a condyle bearing the coxa, the *pleural coxal process* (CxP). Internally (fig. 4) is seen the heavy *pleural ridge* or *entopleurum* (PR), a large ridge-like apodeme lying along the line of the pleural suture, terminating in

the wing process (*WP*) above and the coxal process (*CxP*) below, and bearing a *pleural arm* (*PA*) projecting inward and downward.

Anterior and posterior to the pleural suture, or ventral and dorsal to it when the suture is horizontal, are the episternum (*Eps*) and the epimerum (*Epm*), respectively. These are the two principal plates of the pleurum, and, by their contiguous and infolded edges, they form the pleural suture externally and the pleural ridge internally. The epimerum is nearly always connected, either by an articulation or by fusion, with the lateral part of the pseudonotum (text fig. 3, *PV*).

A study of nymphal pleura (*Melanoplus*, 55, 56) shows clearly that the episternum and epimerum are merely subdivisions of one original plate to which the leg is articulated. Before the wings are developed, the pleural suture does not extend to the dorsal edge of the plate. On the inner surface (55) the pleural ridge (*PR*) is well developed ventrally to strengthen the plate in its function as a supporter of the leg, and the pleural suture is merely the external mark of the formation of the ridge. All the upper pleural structures, the wing process, and the parapteral plates are developed only when the wing becomes functional. In forms with rudimentary wings in the adult stage, such as *Anabrus simplex* (43, 44), these parts are present, but reduced in size. A study of the Chilopoda also appears to indicate that the episternum and epimerum originate as subdivisions of one plate. The lower chilopods, such as *Mecistocephalus* (20), present a number of plates on the side of the segment, one of which (*Pl*) lies immediately over the coxa. The series running through *Scolopocryptops* (21), *Lithobius* (22), and *Cermatia* (23) shows a disappearance of all the other plates, while this one in *Cermatia* (23, *Pl*) becomes divided by a median thickening into two parts resembling the episternum and epimerum of a nymphal orthopteran (56).

Associated with the base of the wing are several small plates lying before and behind the wing process (*WP*). These are the paraptera (*P*). There are never more than two in front of the wing process and they may be called the *episternal paraptera* or the *preparaptera* (*1P*, *2P*). There is generally only one *epimeral parapterum* or *post-parapterum* (*3P*), though some Perlidæ present a second. Voss

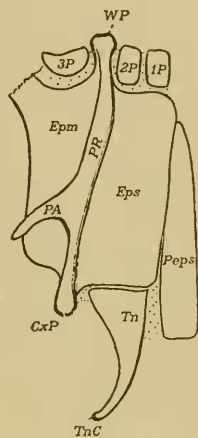


FIG. 4.—DIAGRAMMATIC VIEW OF INNER SURFACE OF THE PLEURUM OF ANY COMPLETE WING-BEARING SEGMENT; *CxP*, COXAL PROCESS OF PLEURUM; *Epm*, EPIMERUM; *Eps*, EPISTERNUM; *1P*, *2P*, EPISTERNAL PARAPTERA OR PREPARAPTERA; *3P*, EPIMERAL PARAPTERUM OR POSTPARAPTERUM; *PA*, PLEURAL ARM; *Peps*, PRE-EPISTERNUM; *PR*, PLEURAL RIDGE (ENTOPLEURUM); *Tn*, TROCHANTIN; *TnC*, TROCHANTINAL COXAL CONDYLE; *WP*, WING PROCESS OF PLEURUM.

(1905) calls the preparaptera the "episternalgelenkplatten," and the postparaptera the "epimeralgelenkplatten." These are excellent descriptive terms but too cumbersome for translation into English or Latin equivalents, and it is well to preserve the name "parapterum" of Audouin.

Either one or both of the episternal paraptera are connected with the head of the costal vein of the wing by strong membrane, and upon their inner surfaces are inserted the strong pronator wing muscles by whose contraction the wing is turned forward upon the pleural wing process and its costal or front edge depressed. In the higher insects there is frequently only one preparapterum present and it very commonly carries a large muscle disc on its inner surface which forms the insertion of the pronator muscle. This whole structure is called the "appareil de pronation" by Amans (1885). The muscle disc may be specifically designated as the *pronator disc* (*PD*). This is not shown in the diagram, for it occurs mostly in the higher orders. As examples of it see illustrations of the Euplexopteran metathorax (98, 100, *PD*), the Coleopteran mesothorax (101, 129), the Coleopteran metathorax (110-121), and the Hymenopteran mesothorax (165). In the Lepidoptera (154) the pronator disc (*PD*) is carried by the upper edge of the episternum, but the parapterum (*P*) is also fused with the latter.

In the Coleoptera there is only one preparapterum present. In the mesothorax it is usually represented by a small inconspicuous plate or rod connected with the head of the elytrum and lying before the wing process (102, 103, 105, 107, 108, *P*), only in rare cases does it bear a pronator disc (101, 129, *PD*). In the metathorax, on the other hand, the disc is always large and prominent (110-121, *PD*). In *Calosoma scrutator* (Carabidae) the parapterum and its disc (110, 113, *P* and *PD*) are loosely articulated to the front of the wing process (*WP*). In *Dytiscus dauricus* (Dytiscidae) the parapterum (114, 115, *P*) is closely articulated to the front of the wing process. In *Hydrophilus triangularis* (Hydrophilidae) the parapterum (*P*) is fused with the base of the wing process (111, 112) and to the anterior edge of a subdivision (*eps*) of the episternum (*Eps*). The line of fusion, however, is easily seen. The same condition is found in *Melolontha vulgaris* (Scarabaeidae) where the base of the parapterum (121, *P*) and the episternal subdivision (*eps*) are closely united. Finally, in such forms as *Cyllene robiniae* (Cerambycidae) and *Dendroctonus valens* (Scolytidae) these two parts (116, 118, *P* and *eps*) are so entirely fused that the line of union is gone. Thus in the higher beetles the appearance of two wing processes (118, *P* and *WP*), carried by the episternum and epimerum, respectively, is produced. The series of forms just described, however, shows conclusively that this condition is secondarily brought about through

the fusion of the base of the parapterum with the front of the episternum. The same thing occurs less conspicuously in several other orders. In the Neuroptera, *Corydalus cornutus* (147) has the single preparapterum (*P*) fused with the upper end of the episternum (*Eps*), thus giving the appearance of there being two wing processes. The same thing is true of the Trichoptera as shown by *Neuronia ocellifera* (146, 148). Even in the Lepidoptera the parapterum (*P*) of *Phassus triangularis* (153) is not really separated from the episternum (*Eps*), and forms a large lobe in front of the wing process (*WP*). Here the base of the wing process sends a long arm (153, 154, *tg.1*) forward and upward to support the tegular plate of the notum (150 *tg*). This, however, is peculiar to the Lepidoptera. It will be observed that in all cases the true wing process can be identified by the fact that it is derived from both the episternum and the epimerum, while the process formed of the parapterum is connected only with the episternum.

The postparapterum or epimeral parapterum (text figs. 3, 4, *3 P*) is of less importance than the preparaptera. It is a small plate of irregular and variable shape lying in the membrane of the base of the wing behind the wing process of the pleurum. It is often lacking, being never present in beetles. It is illustrated in the Corrodentia (82, *3 P*), the Trichoptera (146, 148, *3 P*), the Lepidoptera (149, 153, 154, *3 P*), and the Diptera (174, 176, 179, *3 P*).

In a few of the lower orders a plate frequently occurs before the episternum (text figs. 3, 4, *Peps*). This is the sclerite which Verhoeff (1903) calls the "katopleure" in the Euplexoptera (Dermaptera) and it is well shown in this order by *Spongiphora* (94, *Peps*). But the plate which Verhoeff so designates in the Blattidæ (32, 35, *eps*) would seem to be only a subdivision of the episternum (*Eps*) not comparable with the sclerite in Euplexoptera. The writer formerly (1908) adopted the name "katopleure" for this sclerite, but here substitutes the more appropriate term *preepisternum* suggested by Dr. A. D. Hopkins. The preepisternum falls in line with the presternal element (*Ps*) of the ventral parts (text fig. 3, *Peps* and *Ps*).

The preepisternum is illustrated in the prothorax (26, *Peps*) and the mesothorax (27, 28) of *Spodromantis guttata* (Mantidæ), in the mesothorax (35) of *Ischnoptera hyalina* (Blattidæ), in the mesothorax (43, 44) of *Anabrus simplex* (Locustidæ), in the mesothorax (47) of *Gryllus pennsylvanicus* (Gryllidæ), in the nymphal meso- and metathorax (55, 56) of *Melanoplus*, in the adult (57) of *Hippiscus phanicopterus*, and the adult (70, 71) of *Dissosteira carolina* (Acrididæ), and finally in the mesothorax (94) of *Spongiphora apicidentata* (Forficulidæ). It does not appear to be present in the higher orders, though anterior subdivisions of the episternum occur, especially in the mesothorax of Coleoptera (102, 107, 109). Such

subdivisions, however, are never detached plates, but are simply parts of the episterna equivalent to the superior subdivisions (102, 105, 109, *epm*) of the mesothoracic epimera (*Epm*), and to the subdivisions (111-121, *epm*) of the metathoracic epimera. The writer formerly (1908) wrongly identified this last plate with the postparapterum, a sclerite which is absent in the Coleoptera.

An important sclerite in the pleurum of insects and undoubtedly a primitive plate in the thorax is the *trochantin* (*Tn*). This is a plate lying in front of the coxa (text fig. 3, *Tn*), connected above with the lower edge of the episternum (*Eps*) and articulating below by a small condyle (*TnC*) with the ventral rim of the coxa. Hence, when the trochantin is present, the coxa turns on a hinge line between the coxal condyle of the pluerum (*CxP*) and the coxal condyle of the trochantin (*TnC*). The trochantin is well shown in the Mantidae (26, 27, 28) and in the Blattidae (29, 32, 35). In the latter family it is divided into two parts (*Tn* and *tn*). The smaller part (*tn*) is what Comstock and Kochi (1902) call the "second antecoxal piece," but this part carries the coxal articulation and is, therefore, certainly the principal part of the trochantin.

The trochantin is well developed in the Locustidae (43) and the Gryllidae (46, 47). It is small or rudimentary in the Acridiidae (51, 56). In the Plecoptera its upper end is fused with the episternum in the meso- and metathorax (78, 79). In the prothorax it inserts itself entirely between the episternum and epimerum and the coxa (72, 73, *Tn*), thus separating the latter from its true pleural coxal process. By way of reparation to the coxa, however, the trochantin develops a dorsal coxal condyle (72, 73, 74, *Tn CxP*) in addition to its usual ventral coxal condyle (*TnC*). It even goes further and actually presents an internal trochantinal ridge (74, *TnR*) simulating the true pleural ridge (74, *PR*). This is, of course, a highly specialized condition.

The trochantin occurs in typical form in the Euplexoptera (91, 94, 98, 100). It is present in the prothorax of *Benacus* (Hemiptera) though concealed by the overlapping pleurum (83 *Tn*). In most of the Coleoptera it is a very small plate in the pro- and mesothorax (99, 104, *Tn*) concealed at the upper end of the coxa within the coxal cavity. In the Silphidae (106) and Buprestidae (109), however, it is an exposed plate (*Tn*) occupying the normal position between the episternum (*Eps*) and the coxa (*Cx*). It is absent in the Coleopteran metathorax. In the Neuroptera (147) and Trichoptera (146, 148) it is a large plate. In the Lepidoptera (149, 153, 154, 158, 159) it is partially or entirely fused with the episternum, and is not very distinct from an arm of the sternum (*S*) in front of it. Its ventral coxal articulation is weak or absent. In the Hymenoptera and Diptera the trochantin is either absent or is indistinguishably consolidated with the sternum.

If there is any close relation between the plates of a chilopod segment and those of an insect thoracic segment a study of the former would indicate that the trochantin is really a sternal element. In *Mecistocephalus* (20) the lower half of the coxa is surrounded by a large bilobed lateral subdivision (*Tn*) of the sternum (*S*). In *Scolopocryptops* (21) this plate (*Tn*) is atrophied behind the coxa but articulates with the latter by a special condyle. *Lithobius* (22) shows a similar condition, but here the lower end of the trochantin-like plate (*Tn*) is overlapped by what is the median division of the sternum in *Mecistocephalus*. Verhoeff (1903) calls this plate in the Chilopoda the "trochantin." It is absent in *Cermatia* (23). Börner (1903) regards the trochantin as a "sternales schnürstück" and not as a pleural plate.

Audouin (1824) first specifically applied the term "trochantin" to the plate in *Buprestis gigas* which intervenes between the "epimerum" and the coxa. It happens, however, that in *Buprestis* the episternum presents a number of subdivisions, and Audouin must have included the posterior of these with the epimerum, thus referring to the trochantin as articulating the "epimerum" with the coxa. (See *Buprestis arulenta*, 109; *Tn*.) It will be evident, however, that the plate called "trochantin" by Audouin in *Buprestis* is the plate which in this paper is identified as such in all the orders where it occurs.

Verhoeff (1903) designates as the trochantin the sclerite lying before the coxa and carrying its ventral articulation.

Comstock and Kochi (1902), as already stated, define as the "trochantin," in the Blattidae, a plate which is only a part of the entire trochantin, since it does not carry the ventral coxal articulation. The subdivision of the trochantin bearing the latter is the "second antecoxal piece" of Comstock and Kochi.

Comstock and Kellogg (1902) describe the trochantin as a plate "considered to be an appendage of the coxa between the coxa and the antecoxal piece."

Packard (1896) defines the trochantin as a posterior division of the coxa attached to the epimerum. He refers to the "coxa meron" of Walton (1900) in the Neuroptera, Trichoptera, and Lepidoptera, which is not the trochantin at all, but a subdivision of the epimerum fused with the hind edge of the coxa.

The writer agrees with Verhoeff (1903) in his conception of the trochantin, because this appears to agree with Audouin's original use of the term.

Sometimes small additional plates occur between the trochantin and the coxa. These may be called *accessory trochantinal* or *accessory coxal sclerites*, according as they are associated more with the trochantin or the coxa (91, 94, 98, 100, *Tna*, *Cxa*).

The coxa (*Cx*) is too familiar to need any special description. As already shown (text fig. 3) it is articulated dorsally to the coxal process of the pleurum (*CxP*) and ventrally to the coxal process of the trochantin (*TnC*). The latter may be a sternal element, but it is only in the nymphs of Odonata that the coxa is articulated directly to the sternum (11, 16, *d*). In the Hemiptera and the Coleoptera the upper ends of the coxæ are usually hidden by the overlapping pleurites, but even in such cases the coxa will usually be found articulated to a hidden coxal process of the pleural ridge.

The coxa has often been conceived of as a double structure representing elements corresponding with the episternum and the epimerum. The basis for this idea is furnished chiefly by the Neuroptera, Trichoptera, and Lepidoptera. Here the meso- and metathoracic coxæ of adults are composed distinctly of an anterior and a posterior segment (147, 148, 149, 153, *Cx* and *epm*). Banks (1893) regarded the coxa as derived from two segments, the leg being the appendage of the first in each pair and the coxal spur of *Machilis* representing the appendage of the second segment. Walton (1900) described the two coxal segments as the "coxa genuina" and the "coxa meron." Packard (1898) called the posterior division the "trochantin."

A study of larval and pupal forms in the Neuroptera and Trichoptera shows that this double structure of the coxa is a purely secondary condition. In the larva of *Corydalus cornuta* (144) the meso- and metacoxæ are simple structures like the prothoracic coxa. The epimerum is divided by an oblique groove into an upper plate (*Epm*) and a lower plate (*epm*). In the pupa (145) the lower epimeral subdivision (*epm*) has extended downward behind the coxa (*Cx*) and is partially joined to it. In the adult (147) the lower epimeral plate (*epm*) is entirely fused upon the rear side of the coxa (*Cx*) and, moreover, is separated by a membranous area from the upper epimeral plate (*Epm*). This would appear effectively to dispose of the bisegmental notion of the structure of the coxa in this order. The same developmental process can be shown to take place in the Trichoptera. A pupa of *Neuronia ocellifera* (146) has a long extension (*epm*) of the epimerum (*Epm*) united to the posterior edge of the coxa (*Cx*). In the adult (148) this is separated from the upper part of the epimerum and appears as a posterior segment (*epm*) of the coxa (*Cx*). Probably the same condition could be shown in a freshly pupated Lepidopteran.

Hence, it may be concluded that the double structure of the coxa in these orders is purely a secondary modification and can in no way be used as evidence of a bisegmental origin of the thoracic segments.

3. THE STERNUM.

The writer has not been able to make an extensive study of the sternum. Comstock and Kochi (1902) have recognized three trans-

verse divisions of the chitinous ventral parts and designated them the *presternum*, *sternum*, and *sternellum*. These three parts are shown in the mesothorax of a cockroach (32, *Ps*, *S*, and *St*). The presternum, however, is more commonly present as two small plates lying near the anterior angles of the sternum, the "Vorplatten" of German entomologists. Such plates are present in the prothorax of the Odonata, in a few species of which they unite across the median line in front of the sternum (11, *Ps*), but more usually form two lateral plates separated from the median pre-sternal part (6, 7, 10, *Ps*). In most cases they are, furthermore, fused with the episterna (11, 12, 13, *Ps* and *Eps*). The pre-sternal plates are shown also in the Locustidae (43), the Gryllidae (46, 47), the Perlidae (80), the Corrodentia (82), and in the Forficulidae (91, 94, 98).

From the inner sternal surface there projects dorsally the *entosternum*, consisting most commonly of two chitinous arms, the *furca* (text fig. 6, *Fc*). In some cases the base of the entosternum appears to mark the line between the sternum and sternellum. It is shown to be an invagination by the pit or pair of pits which often marks its location externally (10, 11, *e*). Sometimes the sternum bears also a long median posterior apodemal arm. This is shown in the prothorax of a moth (152, *l*).

V. THE WING ARTICULATION.

The wings are articulated to the body by a simple arrangement of axillary sclerites, two of which hinge upon the anterior and posterior wing processes of the notum while one rests upon the wing process of the pleurum. This is true of all the orders except the Ephemera and the Odonata. These will, therefore, be omitted from the present discussion and described later under the special descriptions of the orders.

Text figs. 1 and 5 sufficiently represent the *axillary sclerites* (1 *Ax*, 2 *Ax*, 3 *Ax*, 4 *Ax*) in their relations to one another, to the notal wing processes, and to the bases of the veins, while fig. 6 shows the articulation with the pleurum. The fourth axillary is usually absent, but since it occurs in the Orthoptera and the Hymenoptera and since, when it is present, the arrangement is more symmetrical, it is included in the diagrams. When it is absent the third axillary articulates directly with the posterior notal wing process. Several other less definite plates usually occur in the central part of the wing base associated with the median, cubital, and first anal veins. These plates, however, are too variable to be given distinctive names and will be referred to in general as the *median plates*.

The membrane of the wing-base may be named the *axillary membrane* (*AxM*). On its anterior margin opposite the base of the costal vein is a small, hairy, semichitinous pad (*Tg*). This, in

the higher insects, develops into a scale-like lobe overlapping the base of the wing. In such cases it is known as the *tegula*, but this name is used in the present paper to designate both the well-developed tegula of the Lepidoptera, Hymenoptera, and Diptera, and its pad-

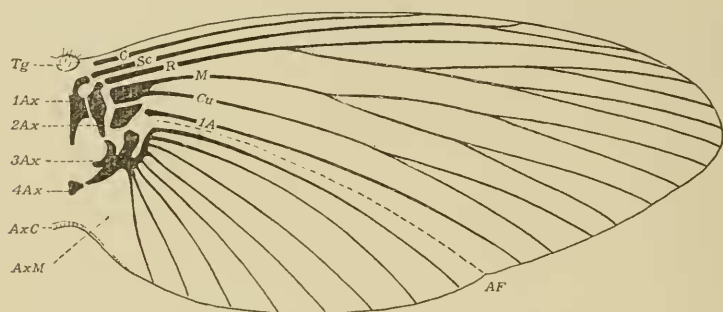


FIG. 5.—DIAGRAM OF A GENERALIZED WING AND ITS ARTICULAR SCLERITES OR AXILLARIES; 1 A, FIRST ANAL VEIN; 1F, FIRST ANAL FOLD; 1 Ax, 2 Ax, 3 Ax, 4 Ax, FIRST, SECOND, THIRD, AND FOURTH AXILLARIES; AxC, AXILLARY CORD; AxM, AXILLARY MEMBRANE; C, COSTA; Cu, CUBITUS; M, MEDIA; R, RADIUS; Sc, SUBCOSTA; Tg, TEGULA.

like representative in other orders. The posterior free margin of the axillary membrane is thickened in such a way that it has the appearance of being a corrugated cord attached to the posterior angle of the notum. It is here called the *axillary cord* (AxC).

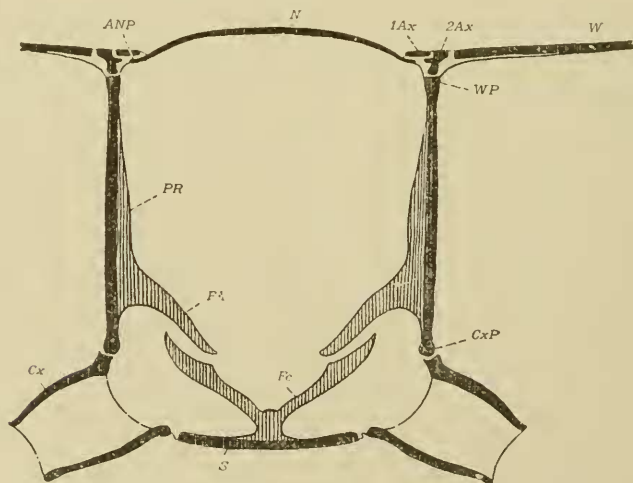


FIG. 6.—DIAGRAMMATIC CROSS SECTION OF A WING-BEARING SEGMENT; ANP, ANTERIOR NOTAL WING PROCESS; 1 Ax, FIRST AXILLARY; 2 Ax, SECOND AXILLARY; Cx, COXA; CxP, COXAL PROCESS OF PLEURUM; Fc, FURCA (ENTOSTERNUM); N, NOTUM; P.A., PLEURAL ARM; PR, PLEURAL RIDGE (ENTOPLEURUM); S, STERNUM; W, WING; WP, WING PROCESS OF PLEURUM.

Occasionally some of the four principal axillaries are subdivided and sometimes there occur small extra chitinizations in the axillary membrane. Thus confusion has arisen through different authors

having based schemes of general nomenclature upon some one form which happens to possess a prominent individual peculiarity.

Jurine (1820) first described in *Xylocopa violacea* the sclerites of the wing base and gave them individual names. The first he called the *grand humeral* in the front wing and the *scutellaire* in the hind wing; the second the *petit humeral* in the front wing and the *diademal* in the hind; the third the *petit cubital* in the front wing and the *furchu* in the hind; the fourth the *naviculaire* which occurs in the fore wing only of *Xylocopa*.

In the same year Chabrier (1820) described the axillary sclerites of *Melolontha vulgaris* and named the three principal ones the *humerus*, the *omoplate*, and the *onguiculaire*, respectively.

The axillaries were next described by Straus-Dürckheim (1828) in *Melolontha vulgaris*. He called them collectively the *epaulieres* in the elytrum and the *axillaires* in the hind wing, while he designated the individual sclerites numerically according to their order in each case. In the wing base of *Melolontha* there are four sclerites, but one of these is an accessory plate not represented in other forms, while the fourth of Orthoptera and Hymenoptera is not present. Hence the individual designations of anterior, second, third, and fourth axillaries used by Straus-Dürckheim can not be consistently applied in the various orders, the third in the *Melolontha* series being an extra piece.

Amans (1885) made a comparative study of the wing articulation in all the insect orders. He recognized three proximal articular sclerites which he named individually the *sigmoïde*, the *median*, and the *terminal*, while he designated as *retro-median* the distal median plate or plates. He accurately described all of them and their relations to surrounding parts. Little can be added to his account.

Lowne (1892) in studying the blowfly called the first axillary the *dens*, the second the *unguiculus*, and two parts of the third the *meta-apterygium* and *deltoid*.

Voss (1905) in describing the external anatomy of *Gryllus domesticus* has given the best detailed account of any one species. Unfortunately, however, the cricket does not afford a typical example of the subject. Although Voss includes in his excellent paper a review of the wing articulation in all the orders, yet he bases his scheme and system of nomenclature on *Gryllus*, in some species of which the first axillary sclerite is divided into two. This same condition occurs also in some of the Locustidæ, but, as far as the writer has observed, is confined to the Locustidæ and the Gryllidæ, and is not constant in either of these families. It certainly can not be regarded as typical. However, the fourth primary axillary is present in *Gryllus*, and Voss's nomenclature is as follows: The two parts of the first axillary and the fourth, which articulate the wing to the back, are named

the anterior, middle, and posterior tergal plates (*Tergalplatten*), respectively; the second, articulating with the pleural wing process, is the middle hinge plate (*Mittlegelenkplatte*); while the third is named the posterior anal hinge plate (*Analgelenkplatte*).

Berlese (1906) in treating of the wing articulation, as in his treatment of the thorax, attempts to line up the parts in four consecutive series corresponding with the division of the tergum. In order to make his scheme consistent, he calls the hairy pad representing the tegula, on the front edge of the wing base, the *acroptero*. The first and second axillaries, though figured as perfectly distinct, are included under the name *proptero*, the third is the *mesoptero*, while the name *metaptero* is given to a rare sclerite in the axillary membrane which does not correspond with the fourth sclerite of Orthoptera and Hymenoptera. The latter Berlese identifies in *Aceridium* as the "mesoptero," although a sclerite is present in *Aceridium* which in every way corresponds with his "mesoptero" of other orders.

The writer retains in the present paper the general term of *axillaries* used by Straus-Dürckheim, and designates the individual sclerites as the *first*, *second*, *third*, and *fourth*, though, as already pointed out, this enumeration does not correspond with that of Straus-Dürckheim. (For synonymy see Glossary.)

It will not be necessary to describe in detail the axillary parts in each order. They can be sufficiently made out by a study of plates 47, 48, 64-69, and a comparison with text figs. 1 and 5 will show the general plan which prevails. The four principal axillaries are indicated by the numerals 1, 2, 3, and 4; by the abbreviations 1 *Ax*, 2 *Ax*, 3 *Ax*, and 4 *Ax*; or by shading in transverse lines for the first and fourth, in oblique lines for the second, and in longitudinal lines for the third. The median plates are indicated by broken oblique lines. The articulation of the sclerites to the notum is shown in figs. 75, 90, 96, 127, 128, 129, 131, 136, 150, and 161, and by text figs. 1 and 6.

The wing base is a difficult subject to illustrate because the small sclerites are so easily turned in slightly different positions and then present very different appearances. Most of the drawings have been made by getting first a camera lucida sketch of the specimen mounted in water or glycerine and flattened out under a cover glass, and then drawing in the details from dissections and a closer examination under a binocular microscope. But perhaps a dozen different drawings could be made from the same specimen all differing in details. The following are general descriptions of the specific characters of the various elements of the wing base.

The tegula (Tg).—This is usually a membranous or semichitinous pad-like lobe developed on the anterior membranous part of the wing root near the base of the costal vein. It is nearly always made con-

spicuous by the long hairs upon it. (As typical examples see 60-63, 185, 186, 188, 200, *Ty*). In the Diptera, Hymenoptera, and Lepidoptera the tegula is highly developed in the mesothorax as a large scale-like lobe overlapping the base of the wing. (Diptera, 210, 212; Hymenoptera, 205, 206; Lepidoptera, 149, 150, 202). In the Lepidoptera the tegula is so large that it is supported by a special plate of the mesonotum (150, 156, *ty*), which in turn is supported by a large tegular arm (153, 154, *tyA*) from the base of the pleural wing process (*WP*).

The tegulae of the Lepidoptera must not be confounded with the *patagia* which occur in some families of this order. The *patagia* are large thin lobes developed on the pronotum and are specially well developed in such genera as *Agrotis* and *Geometra*. They are simply thin expansions of the pronotum. In *Agraulis* they may be seen in an intermediate condition.

Lowne (1892) uses the term "epaulet" for the tegula of the blowfly. He says that it does not correspond with the tegula of the Hymenoptera. They certainly have identical situations on the wing base, however, and it is hard to see how they could be independent organs. Lowne's objection is based on the relative position of the anterior spiracle, but the spiracle belongs to the pleurum and its position in the two orders is different on account of the different modifications of the pleurites. It is the spiracle that is shifted and not the tegula.

The first axillary (1, 1 Ax, transverse shading).—This sclerite is supported by the anterior notal wing process (*ANP*) and can readily be determined by this connection. It consists of a flattened body articulating externally with the second axillary, and of a curved anterior neck which abuts against the head of the costal vein (*C*). In some cases the neck is absent and then the first axillary is separated from the costa. Sometimes, as in a few Orthoptera, the neck is detached from the body and appears as an independent sclerite.

The second axillary (2, 2 Ax, oblique unbroken shading).—This is the pivotal sclerite of the wing base, that is, the one by means of which the wing rests and turns upon the wing process of the pleurum (text fig. 6). The articulation is generally by means of a large ventral process of the axillary which fits against an articular surface on the posterior side of the wing process. The dorsal surface of this sclerite articulates by a long ridge with the outer edge of the first. Its anterior end is usually associated with the head of the radial vein of the wing (*R*), being either fused with it or contiguous to it (text figs. 1, 5). There is generally a large muscle disk attached by a ligament either directly to the posterior end of the second axillary (199, *MD*) or to the axillary membrane near it. In an exceptional case (*Cytlene* 140) it is attached to a special process of the notum (*o*). The ven-

tral end of the muscle inserted upon this disk is attached to the anterior edge of the metacoxa in beetles. This is probably the principal muscle concerned in bending the wing toward the body.

The third axillary (3, 3, Ax, longitudinal shading).—This sclerite serves principally as a means of folding the anal region of the wing. When the fourth is absent it articulates directly to the posterior notal wing process. It nearly always presents a scoop-like muscle process on the side next the body at right angles to its long axis. The muscle inserted upon this turns the third axillary on its axis and thus causes a folding of the anal region of the wing. In the beetles this muscle is attached by a ligament first to a smaller accessory sclerite. The outer edge of the third axillary is always connected with the bases of the anal veins; frequently the latter are fused with it by a common flexible chitinous base.

The fourth axillary (4, 4, Ax, transverse shading).—When this small sclerite is present it forms the posterior hinge plate of the wing, intervening between the posterior notal wing process (*PVP*) and the third axillary.

The median plates (oblique shading in broken lines).—These lie between the base of the radius (*R*) and the third axillary. They are variously developed but are principally associated with the bases of the media, the cubitus, and the first anal when the latter is separated from the other anals. Often one of them is fused with the third axillary and sometimes none of them is present.

The axillary membrane (AxM).—This is specially developed along the anal margin of the wing base where it is bordered by the axillary cord. It nearly always forms an ample expansion here, but in the wings of flies and the elytra of beetles it forms large folded lobes. These are called the *squamæ* or *alulæ* in the Diptera (212, *Al*). The similar membranous lobes under the elytra of some beetles (131, *Al*) are certainly the same things as the alulæ of Diptera. Comstock and Needham (1898) have already suggested this and cited the marginal cord-like structures (131, *AxC*) arising from the posterior angles of the scutellum as evidence.

Axillary cord (AxC).—This is the corrugated cord-like thickening along the posterior margin of the axillary membrane. The pair, one on each side, originate from the posterior lateral angles of the notum, and are thus valuable marks in determining the limits of this plate when the latter is obscured by close connection with the parts following.

The wing veins (C, Sc, R, M, Cu, A).—Most of these are connected or associated in a very definite and constant manner with the sclerites of the wing base. The latter are certainly a valuable asset in the identification of the veins in the different orders. Comstock and Needham (1898, 1899), however, have left little to be said on this

subject, and a study of the axillaries simply confirms the results of these authors derived from a study of the venation itself.

The general relation of the veins to the axillaries is shown in text figs. 1 and 5. The *costa* (*C*) does not connect with any of them. Its base very generally forms a separate piece from the main costal shaft, and is connected by strong membrane with the preparaptera of the pleurum. This separated costal head will be seen clearly by a review of Plates 64-69.

The head of the *subcosta* (*Sc*) articulates with the anterior end of the neck of the first axillary, except in rare cases of special modification. (For typical examples see 184, 187, 201, 206.) The base of the *radius* (*R*) is nearly always more or less closely fused with the base of the subcosta (*Sc*), but it is clearly connected also in a great many cases with the anterior end of the second axillary (182-184, 185, 186, 192, 198, 203, 204, 208). In other examples its head is only contiguous to the third axillary (185, 188, 191, 202, 209, 210, 211, 212). In a few beetles the radius and second axillary are separated by a wide membranous space (193, 194).

The *media* (*M*) and the *cubitus* (*Cu*) are closely associated with each other at their bases and with the median plates. A simple arrangement is shown in the wings of *Corydalis cornuta* (200, 201). But both the media and the cubitus are so frequently fused with the radius that their basal parts are difficult to determine in a definite manner (186, 187, 202, 203, 205, 206, 207). In other cases they are perfectly distinct at their bases (192, 194, 195, 198, 200).

The *first anal vein* (1*A*) is separated from the rest of the anals in the Orthoptera by the *anal fold* (see figures on Plates 47, 48). The only apparent exception to this noted by the writer is in the front wing of *Gryllus* (67). In the wing of a nymphal mantid (59) the first anal (1*A*) clearly arises at the base of the wing, independent from the rest of the anals. Comstock and Needham (1898, '99) have shown the same thing in a drawing of the wing of a cockroach nymph. The other anals generally arise from a common base, which is connected or fused with the third axillary. The *vena dividens* (60, *D*) is not a primary anal, but a secondary vein developed in the first anal fold (62, 64, 66, 1*F*). In most other orders the anals are fewer, and the first is not specially separated from the rest.

The peculiar structure of the base of the wing in dragonflies will be described under the Odonata in Section VII.

VI. GENERAL CONCLUSIONS.

1. The fourth head segment, apparent in some of the lowest insects, is still regarded as a doubtful metamere by some embryologists. Assuming its genuineness, the following general statement seems pretty well established: The head of insects is composed of six con-

solidated primary segments, with the appendages of the following or neck segment attached to it forming the labium, and sometimes also with the sternum of this segment intimately fused into its ventral surface forming a gular sclerite.

2. The microthorax is formed from the embryonic segment immediately following the last of the consolidated head metameres. It is the segment of the neck of the adult. Its sclerites form the cervical sclerites of the neck, often reduced or rudimentary, and the gular plate of the head when such a plate is present. Its appendages always fuse with each other, and become closely associated with, generally attached to, the base of the head, and constitute the labium.

3. The thorax proper consists of three segments, or of three with the tergum of the first abdominal segment added in the Hymenoptera. These three segments are primary metameres, and there is no real evidence of each having been formed through a fusion of two or more primitive segments. The original thoracic region may have consisted of more than three segments, but if so, the extra segments have disappeared and have taken no part in the formation of the thoracic sclerites in modern insects.

4. The thoracic sclerites in all insects conform to one definite plan represented diagrammatically in fig. 3. The sclerites are subdivisions of the wall of one primitive segment, and the apparent double nature of each segment is secondary. Characters that have been urged as special evidence to the contrary, such as the equivalence of the episternum and epimerum and the double structure of the coxa in some orders, lose their significance when nymphal, larval, and pupal forms are examined. The episternum and the epimerum are subdivisions of one original plate on the side of the segment, and the posterior segment of the coxa shown by some orders is simply a detached piece of the epimerum fused upon the coxa in the adult stage.

5. The primitive tergum is a single undivided plate from the entire lateral margins of which the wings arise. This simple tergal structure is shown by the nymphs of all the lower insects and by many larvæ and pupæ and by the adults of Orthoptera. In the adults of all the other principal orders, however, there is present behind this wing-bearing plate or true notum a second tergal plate, the postnotum or pseudonotum, developed in the intersegmental membrane of the nymph or pupa, having no connection with the wings, but attached to the upper ends of the epimera.

The notum presents three fundamental ridges on its ventral surface as shown in text fig. 2. Its subdivisions do not, in most cases, closely conform with these ridges, nor do they strictly correspond in all the orders. They are in general similar but not necessarily homologous.

6. The pleurum consists fundamentally of a plate strengthened internally by a heavy, inflected, median, vertical ridge to support the wing above and to carry the leg below. Thus it has become divided into the episternum anteriorly and the epimerum posteriorly, separated externally by the pleural suture along the line of the internal pleural ridge. (See text figs. 3 and 4.) The wing support forms a wing process and the coxal support the coxal process of the pleurum. In front of the episternum there is in some of the lower insects a pre-episternum. Along the base of the wing parapteral plates are developed. In front of the coxa is the trochantin, a plate possibly derived from the sternum, articulating above with the episternum and below forming the ventral articulation of the coxa.

7. The wing is hinged to the notum on the two notal wing processes, and is supported from below upon the wing process of the pleurum.

In the Ephemera and Odonata the chitinous wing base is directly continuous with the walls of the thorax. In all other orders there is an articulation formed by several axillary sclerites in the membranous base of the wing. Three of these are of definite characteristic shape and of constant recurrence in all the orders and are present in the elytra of beetles and the halteres of flies. In the Orthoptera and Hymenoptera a fourth sclerite occurs, and this number may be regarded as the full complement. When four are present the first and fourth articulate with the anterior and posterior notal wing processes, respectively, the second articulates with the wing process of the pleurum, while the third supports the anal veins and is concerned in the plication of the anal region when the latter is folded. Where the fourth is absent the third articulates with the posterior notal process.

VII. SPECIAL CHARACTERS OF THE ORDERS.

A. CHILOPODA.

A study of the Chilopoda in connection with a study of the insect thorax brings out the following two interesting features:

1. A serial examination of the pleurum of *Mecistocephalus* (20), *Scelopocryptops* (21), *Lithobius* (22), and *Cermatia* (23) appears to indicate that only one plate (*Pl*) of the numerous pleurites on each segment in the lower Chilopoda (20) persists in the higher (23), and this plate is suggestive of being the one from which the episternum and epimerum of the Hexapoda are formed. Compare *Cermatia* (23, *Pl*) with the *Melanoplus* nymph (56, *Eps* and *Epm*).

2. The trochantin (*Tn*) appears to be originally a lateral subdivision of the sternum (20). The part behind the coxa disappears (21, 22) while the part in front extends upward to the pleurites. In *Cermatia* (23), however, it is gone entirely.

These points are simply suggestive and it is not claimed that a close relation necessarily exists between the Chilopoda and the Hexapoda. Verhoeff (1903), however, goes further than this and identifies both the episternum (coxopleure) and epimerum (anopleure) with separate plates of the chilopod plenrum.

B. HEXAPODA.

I. APTERA.

Since the importance of this order is philosophical rather than practical, the author has not devoted much time to its study. Moreover the external anatomy of the thorax in the three principal genera has been thoroughly exploited by Verhoeff (1903, 1904a).

As is well known, the Japygidae possess a small intercalary tergal plate between the pronotum and the mesonotum and another between the latter and the metanotum. By many authors these are regarded as rudiments of primitive segments and the primitive thorax is conceived to have been composed of three pairs of segments described and named by Verhoeff (1903c, 1904a) as follows: The microthorax and prothorax, the stenothorax and mesothorax, and the cryptothorax and metathorax. But this subject has been discussed in Section II, dealing with the segmentation of the head and body (p. 519).

Verhoeff (1903) describes the pleura of all three segments of *Japyx* as very similar to the pleurum of *Lithobius*. He shows in *L. forficatus*, however, two plates above the one attached to the coxa (22, *Pl*) instead of one as shown by the species figured in this paper (22). The microthorax is represented by a sternal plate only. In *Lepisma*, according to Verhoeff, the prothoracic pleura have all the parts of the pleura of Blattidae and Euplexoptera (Dermaptera), but the parts are rudimentary in the mesothorax and the metathorax. The microthorax in this genus, also, consists of a large sternum but has no pleural or tergal plates. In *Machilis* the three segments differ much from those of either *Japyx* or *Lepisma*. The microthoracic sclerites and the pleurites of the other three segments are almost lacking, while the terga are largely developed and reach far down on the sides of the thorax.

In *Japyx* each thoracic segment bears a spiracle, while a fourth spiracle is present close to the lateral margin of the mesosternum and near its posterior edge. Hence, this spiracle must be the spiracle of a degenerate segment.

Verhoeff (1903) regards the Thysanura not as insect "progenitori," but as a degenerate residuary branch of the primitive wingless insects. This view is undoubtedly the correct one.

II. EPHEMERIDA.

Species studied.—*Heaegenia bilineata* (1, 2, 3, 4).

Characteristics.—Shows little similarity to other orders of insects, except to Odonata, which are suggested by structure of wing articulation. Notum and pseudonotum present in mesotergum and metatergum. Lateral parts of mesonotum (4) complicated by irregular confusion of elevations and depressions. Axillary cords (*Ax C*) arising from middle of posterior edge of notum, pseudonotum hidden from above. On mesopleurum (1) wing process (*WP*) and pleural suture (*PS*) present, but episternum and epimerum are regions not definitely defined as plates. Epimeral region continuous with pseudonotum (*PV*). Wing veins flexible at base, merging into edges of tergum. Only one axillary sclerite developed (4, *1Ax*). Metatergum smaller than the preceding (3), both notum and pseudonotum present. Metapleurum with distinct wing process (*WP*), but without definitely formed pleurites or pleural suture.

III. ODONTA.

Species studied.—*Libellula auripennis* (5, 6, 18, 19), *L. pulchella* (16), *Pachydiplax longipennis* (7, 10, 15, 17), Libellulidae: *Lestes uncatatus* (8, 9), *Enallagma durum*, Agrionidae: *Gomphus brevis* (11, 13), *G. plagiatus* (12, 14), Eschmidæ.

Characteristics.—1. Microthorax represented in both nymphs and adults by a number of plates on sides of the neck (5, 6, 8, 9, 12, *mi*, 1 *mi*, 2 *mi*, 3 *mi*, 4 *mi*) closely associated with side of the prothorax and forming a long arm on each side of neck reaching forward into concavity of the back of head.

2. Pronotum topographically divided into three distinct transverse lobes (5, 7, 8, 9, 12, 13, *N*), the third often with a descending postepimeral strip (5, 7, 12, *a*).

3. Prothoracic pleurum shows an evolution from such simple forms as shown by nymph of *Lestes uncatatus* (8) and adult of *Pachydiplax longipennis* (7) to forms such as *Gomphus plagiatus* (12) and *Gomphus brevis* (13) where epimerum (*Epm*) forms principal plate on side, episternum being divided into a small upper piece (*eps*) fusing with epimerum (12), and into a larger ventral plate (*Eps*) fused with lateral plate of presternum (*Ps*).

4. Presternum (*Ps*) of the prothorax varies from a transverse plate with expanded lateral part (11), to a condition where it consists of two plates independent of the sternum and lying at sides of the latter (5, 6, 7, 9, 10). These plates in some forms, as shown under 3, completely fuse with lower subdivision of episternum (11, 12, 13).

5. Prosternum connected with the mesosternum by two slender rods (6, 7, 10, 11, 18, *b*).

6. Prothoracic spiracle plates closely associated with mesothorax in the nymph (14, 16, *Sp*). In the adult they unite with each other across the back, thus forming a complete spiracular dorsum (18, *g*) which fuses with mesothorax in front of declivous part of the latter formed by dorsal parts of episterna.

7. Trochantin lacking in both nymphs and adults.

8. Coxæ of all the segments in the nymphs articulate ventrally with the sternum by a special condyle (11, 16, *d*).

9. Episterna of mesothorax and metathorax subdivided in both adults (18, 19) and nymphs (14, 16) into an upper plate (*eps*) and a lower plate (*Eps*). In mesothorax the upper meets its fellow of opposite side along the mid dorsal line between the true mesonotum and the prothoracic spiracular bridge (18 *g*). An old nymph (14) shows an intermediate condition of this modification. In metathorax the upper plate of episternum (*eps₃*) fused with preceding epimerum (*Epm₂*). Hence, the two oblique sutures on side of combined meso- and metapleura are the two pleural sutures (16, 18, *PS*), while the incomplete middle one is the remnant of the intersegmental suture. In metathorax the epimera (18 *Epm*) meet each other along the mid ventral line behind metasternum, just as do episterna of mesothorax in front of mesotergum.

10. Pleural wing process (18, 19) divided into two arms, the posterior of which is the true wing process (*WP*) articulating with wing, while the anterior (*h*) is an arm supporting the large costal lobe of humeral angle of the wing.

11. The flexible bases of wing veins (17) merge into edges of notum as in Ephemera. Only one distinct axillary is present (17, *Alex*). Base of the costa (17, 181, *C*) forms a large tripartite lobe at humeral angle of wing supported on anterior arm (*h*) of wing process (18, 19). Median point of wing base, formed principally by base of radius, articulates, by a ventral process, with true pleural wing process (18, 19, *WP*). This process thus corresponds with second axillary of other orders.

Lendenfeld (1881) has made an exhaustive study of the details of the thoracic structure and the wing articulation in Odonata. If the reader is interested in minutiae and in cumbersome Latin names he is referred to the work of this author. Lendenfeld's nomenclature can not be adopted because it is not based on the idea of serial segmental homology.

The muscles of the wings in Odonata differ from those of all other orders in being inserted upon the bases of the wings instead of upon the neighboring parts of the notum and pleurum. As described by Lendenfeld (1881) the set of eight muscles in each wing are as follows: (1) *Abductor*, (2) *pronator radii primi*, (3) *flexor*, (4) *flexor radii quinti*, (5) *adductor radii quinti*, (6) *pronator*, (7) *supinator*.

(8) *tensor*. All of these but (5) are attached to the sclerites of the pleurum and all but (8) are inserted upon the base of the wing either directly or by long tendons. (5) arises from a process of the notum, while (8) is inserted not upon the wing base but upon neighboring plates of the notum.

IV. ORTHOPTERA.

Species studied.—*Spodromantis guttata* (24, 25, 26, 27, 28, 30, wings 61, 62), Mantid nymph (34, 39), Mantidæ; *Byrsotria fumigata* (29, 32, 33, 34), *Ischnoptera hyalina* (35, 36, 37), *Blutella germanica* (38, 40, wing bases 185, 186), Cockroach wing, diagrammatic (60), Blattidæ; *Microcentrum laurifolium* (39, 41, wings 63, 64), *Anabrus simplex* (42, 43), Locustidæ; *Gryllus pennsylvanicus* (45-50, wings 66, 67, 188), *Gryllotalpa borealis* (wing 65), Gryllidæ *Melanoplus femur-rubrum* (51, 52), *Melanoplus* nymph (55, 56, 58), *Hippiscus phoenicopterus* (53, 54, 57), *Dissosteira carolina* (70, 71, wings 68, 69, 187, 189), Acridiidae.

Characteristics.—1. Microthoracic sclerites of neck present in nearly all species and often highly developed, consisting of tergal, pleural, and sternal plates.

A good example is afforded by *Spodromantis guttata* (24, 25). The tergal plate is in this species a narrow U-shaped band (24) open posteriorly, but the pleural plates are so large that they greatly encroach upon the dorsal surface of the neck. The pleurites form a series of four sclerites on each side (25), the two of the third pair meeting each other on the mid ventral line. Anterior to these are two transverse sternal plates. The submentum (25, *Sm*) is clearly supported by the pleural and sternal microthoracic sclerites.

The microthorax of Blattidæ, as represented by *Ischnoptera hyalina* (36, 37), is similar to that of the Mantid. Here, however, the tergal sclerites have the more usual form of two narrow longitudinal plate (36). In *Gryllus* (45) the sternal plates are broken up into two transverse series of smaller sclerites. The labium (*Sm*) is here, also, closely associated with the microthoracic plates. *Anabrus simplex* has only one plate on each side of the neck. In the Acridiidae there is a chain of three small cervical sclerites (51, *Mi*) on each side connecting the head with the prothorax.

2. Pronotum in general shows a tendency to crowd out the pleurites of its segment by a downward growth on each side over pleural regions.

In the lower families this is less evident and in the Mantidæ (26) and Blattidæ (29) the propleurum presents all the parts of any complete generalized pleurum, namely, an episternum (*Eps*), an epimerum (*Epm*), a preepisternum (*Peps*), and a trochantin (*Tn*) carrying the ventral coxal articulation (*TnC*), also a pleural suture

(*PS*) separating the episternum and epimerum externally, and a pleural ridge internally. In *Gryllus* (46) the parts are highly modified, but all are represented. The pleural ridge develops a large scapula-like internal plate (*P.1*) lying within the notum. In *Anabrus* the preepisternum is not a distinct plate. It is when the Acridiidae are reached, however, that the greatest modification is found. Here the pronotum (51) extends downward on the side to the base of the leg reducing the episternum (*Eps*) to a small plate in front of the coxa, and the epimerum (*Epm*) to a small plate behind the coxal articulation and fused to the notal rim. A rudimentary trochantin (*Tn*) is also present.

In thus usurping the territory of the pleurum the pronotum has also taken over the function of the former and has become modified accordingly. An inner view (52) shows a prominent pseudopleural notal ridge (*NR*) bearing an arm (*NA*) near its lower end, just as does a normal pleural ridge (see 44, 55), and terminating below in a pseudopleural coxal process (*NCoP*) to which the coxa is articulated. A large posterior reduplication (*Rd*) back of the posterior groove and ridge (51, 52, 2) overlaps a large part of the mesothorax.

The Acridiid pronotum is thus highly specialized, doing duty as both notum and pleurum, and its subdivision into four transverse parts can not reasonably be cited as a typical example of the quadruple structure of the insect tergum. Yet it is invariably used to illustrate the prescutum, scutum, scutellum, and postscutellum. But it is clearly illogical, as shown in another part of this paper, to offer as "typical" an example that is confessedly not so!

3. Meso- and metapleura closely resemble each other. In most cases illustrations of either one will serve for both.

In the Mantidae (27, 28) the pleural suture (*PS*) is nearly horizontal, but otherwise the meso- and metapleurum is of the typical generalized form. (Compare 27, 28, with text figs. 3 and 4.) In Blattidae (*Byrsotria fumigata* 32) the pleural parts are modified on account of the flattened shape of the body, but in a side view (*Ischnoptera hyalina* 35) the typical structure can be made out. The pleural suture (*PS*) separates the small dorsal epimerum (*Epm*) from the larger ventral episternum (*Eps*). An internal view (33) shows a pleural ridge (*PR*) and arm (*P.1*) in normal relations to the other parts. One preparapterum (*P*) is usually present, and below this an indistinct preepisternum (35, *Peps*) fused with the episternum (*Eps*). At least it is evident that if a preepisternum is present it must occupy some such position. Yet Verhoeff (1903) regards the subdivision (*eps*) on the posterior edge of the episternum (*Eps*) as the "katopleure," while the plate he so designates in the Euplexoptera lies before the episternum. This Euplexopteran sclerite (94, *Peps*), then, is Verhoeff's "katopleure" or the preepisternum (*Peps*) of the

present paper. Now, to homologize the preepisternum of the Euplexoptera (94, *Peps*) with this posterior subdivision (*eps*) of the Blattid episternum (32, 34, 35) requires too much anatomical contortion, and the writer prefers to call the subsclerite in question (*eps*) simply a part of the episternum (*Eps*). Comstock and Kochi (1903) call it the "second antecoxal piece," but it is unnecessary to give it even this designation, which is also undesirable, because misleading.

The trochantin of the Blattidæ is likewise subdivided by an oblique suture into a dorsal part (35, *Tu*) and a ventral part (*tn*). The latter is identifiable as the trochantin by its coxal articulation (32, 35, *Tn'*). Comstock and Kochi (1902) call it "the antecoxal piece." Verhoeff (1903) recognizes it as the trochantin.

In the Locustidæ (43, 44), the Gryllidæ (47) and the Acridiidæ (57, 70, 71) the preepisternum (*Peps*) is separated from the episternum by a more or less distinct, though variable, suture. This interpretation may appear doubtful, but a line is distinct in the Acridiid nymph (55, 56) separating a large preepisternum (*Peps*) from the episternum (*Eps*). In *Anabrus* (43) the preepisternum (*Peps*) falls in line with the presternal plate (*Ps*).

A study of nymphal forms (55) shows that the paraptera (*P*), the upper end of the pleural ridge (*PR*), and the wing process are developed only in connection with the adult wing. Short-winged adults, however, such as *Anabrus simplex* (43, 44), have these parts (*P*, *WP*) present, though somewhat rudimentary.

4. Meso- and metanotum similar in most cases and often structurally identical.

In *Blatella* (38, 40) each is so simple in its construction that it could be taken as a diagram of the generalized notal plan of structure. (See text figs. 1 and 2.) Ventrally (40) it presents simple anterior and posterior marginal notal ridges (*AVR*, *PVR*), the latter at the front of a posterior reduplication (*Rd*), and a median V-shaped ridge (*V*) or "entodorsum" of Amans (1885). These three ventral ridges form lines on the surface (38, *anr*, *v*, *pnr*) marking off four apparent notal subdivisions. The metanotum of a short-winged female of *Gryllus pennsylvanicus* is very similar (50); that of a long-winged form differs in shape and has the anterior phragma (*Aph*) highly developed, but is yet of the same fundamental generalized type. In *Microcentum* the V-shaped ridge (*V*) is rudimentary in both mesonotum (41) and metanotum (39), while in the Mantid adult (30) and nymph (31) its apex continues forward as two parallel median ridges to the anterior marginal notal ridge. In Acridiidæ (54) there is present an extra ventral ridge (*ss*) consisting of two arms diverging outward and forward from the middle of the posterior notal ridge (*PVR*). The arms of this ridge (*ss*) cross over the arms of the flattened and almost obsolete V ridge (*V*). Their

bases form lines on the dorsal surface (53 *s*) which mark off two oval posterior lateral areas not represented in other families.

If the four divisions of the notum (38), as marked out by the three ventral ridges (40), are called the prescutum, scutum scutellum, and postscutellum, it must be borne in mind that they are not homologous with the divisions so named in the tergum of Lepidoptera, Hymenoptera, and Diptera. The first division is a narrow marginal strip carrying the prephragma (*1ph*) when this is present. The second is a large bilobed plate carrying both the notal wing processes (*1NP*, *PNP*), the third consists of a triangular median area and of two posterior lateral arms, the fourth is a posterior marginal band consisting of the posterior reduplication (*Rd*) and terminating laterally in the axillary cords (*1ac*). This last subdivision can in no way be identified with the "postscutellum" of other orders, such as Coleoptera—the representative of this plate is lacking in Orthoptera.

5. Pseudonotum absent in both mesothorax and metathorax. Posterior marginal part of notum, which some entomologists have called "postscutellum" in Orthoptera, *not* the homologue of this plate in other orders.

In many Orthoptera, especially the Acridiidae (57), the first abdominal tergum (*1T*) presents an anterior subdivision (*1t*) whose median dorsal part fuses with the metanotum, but whose lateral parts are mostly free from the metathorax, and on each side enter into the formation of an arm of the first abdominal tergum, extending downward before the auditory organ (*1tu*). Internally, on the line between these two subdivisions of the first abdominal tergum, is a prominent ridge. In other Orthoptera this anterior subdivision and the ridge are less developed, in some cases it amounts to only a thinner anterior area which is overlapped by the reduplication of the metanotum.

This abdominal tergum could claim no place in the present discussion were it not that many entomologists have regarded its anterior subdivision as a part of the thorax. Voss (1905), for example, has identified it as the pseudonotum (postsentum, Voss) of the metathorax and the internal ridge as the postphragma. The part in question, however, and the main plate of the first abdominal tergum (57, *1t* and *1T*) are unquestionably anatomically continuous. Moreover, the first is best developed in the Acridiidae, while in Blattidae it is represented only by the weakly chitinized anterior half of the tergum overlapped by the metanotum, a subdivision such as all the abdominal terga present. Berlese (1906) regards it as a part of the first abdominal tergum, but he also thus identifies the pseudonotum (postscutellum) of the metathorax in Coleoptera. The present writer, however, sees no reason for regarding these parts in the two orders as the same. Any one can see that they are not similar in appearance, and that their

anatomical structure and relation to the surrounding parts are different. Therefore, why not call one a part of the abdomen, which it actually is, and the other a part of the thorax, which it actually is?

6. Wing articulation of typical generalized type, generally four axillary sclerites present, bases of the veins mostly distinct (60-69, 185-189).

In some cases the first axillary is divided into two as in Locustidae (*Microcentrum laurifolium*, 63, 64). Voss (1905) describes the same thing in *Gryllus domesticus*. In *G. pennsylvanicus* the neck of the first axillary is joined to the body of the sclerite by very delicate chitin, but the two parts can be demonstrated to be continuous (188).

The venation presents many modifications, but each form possesses some character which, used in strict conformity in all the families, furnishes a clue for the identification of the veins. (See Plates 47, 48, 65.) An important character is the location of the first anal fold (*AF*) in which the vena dividers (*D*) is located when the latter is present (58, 69, 185, 186, 189, *D*). It will be noticed that in all cases, except in the fore wing of *Gryllus* (67) the first anal vein (*1A*) lies in front of the anal fold (*AF*) or the vena dividers (*D*) and is independent of the rest of the anals at the base. That this is a nymphal condition is shown by the nymphal Mantid wing (59). Comstock and Needham (1898, '99) have illustrated the same thing in the wing of a young cockroach. Thus the first anal vein can be identified by its lying before the first anal fold and by its basal independence. Likewise its absence can be proved in the fore wing of *Gryllus* 67. The anal fold here appears to lie before the cubitus (*Cu*) but basally it will be found originating behind this vein. In the hind wing of the same species (66) the anal fold and first anal are normal. The first anal is frequently branched (60, 64), while in *Dissosteira* it fuses basally with what appears to be the vena dividers of the hind wing (69, 189).

The cubitus (*Cu*) and media (*M*) show a tendency to unite with each other at their bases, as illustrated in Blattidae (60), Mantidae (62), Locustidae (63, 64), Gryllidae (67), and Acrididae (68, 187). In the hind wings of *Gryllus* (66) and *Dissosteira* (69) the media (*M*) is fused for some distance with the radius (*R*). That the vein labeled *M* is the media in these wings can be determined by comparison with the venation of the fore wings (67, 68), where the media is separate from the radius at least to a point proximal to its union with the cubitus. In the fore wing of the Acrididae (*Dissosteira* 68) the costa (*C*) forms the anterior margin, while the subcosta (*Sc*) is clearly double from near the base. It is, hence, clear that in the hind wing the costa is absent and that what is here the marginal vein is the first branch of the subcosta (*Sc*).

It is interesting to observe that the tegula (*Tg*) is represented in both the fore and hind wings of nearly all Orthoptera by a small hairy pad on the axillary membrane between the base of the costa and the attachment to the notum.

V. PLECOPTERA.

Species studied.—*Pteronarcys californica* adult (72, 75, 78, 79, wings 182, 183, 184). *Taniopteryx fasciata* adult, *Perla* sp. nymph (73, 74, 76, 77). *Acroneuria* sp. nymph (81), *Isogenus* sp. nymph (80).

Characteristics.—1. Microthorax not well developed, consisting generally of a chitinous band or plate on each side of neck.

2. Trochantin (*Tn*) of prothorax in both nymphs (73) and adults (72) inserts itself between coxa and true pleurum formed of episternum (*Eps*) and epimerum (*Epm*). Upper part of trochantin (*Tn*) then takes on both the function and appearance of the displaced pleurum. It articulates with dorsal edge of coxa by a special condyle (*Tn CxP*), presents externally a pseudopleural trochantinal suture (72, *Tn S*) and internally a pseudopleural trochantinal ridge (74, *Tn R*). Continuing above the latter on true pleurum is the real pleural ridge (*PR*).

3. Trochantin of both mesothorax and metathorax fused in adults (78, 79, *Tn*) with episternum (*Eps*), apparently not taking part in coxal process (*CxP*). A nymph of *Acroneuria* (81) is similar but one of *Isogenus* (80) presents a very typical trochantin (*Tn*) in the mesothorax.

4. Wing bases very simple, parts of typical arrangement (182, 183). A triangular plate (*C*) of head of costa articulates with parapterum (78, 79, *P*). Wing venation shown by figs. 183, 184.

5. Meso- and metanotum divided topographically into regions (75) but not by lines or sutures. V-ridge absent.

6. Plecoptera differ from Orthoptera in specialized condition of prothoracic pleurum and in development of pseudonotum in both meso- and metatergum.

VI. CORRODENTIA.

Species studied.—*Crastospinus venosus* (82).

Characteristics.—1. Microthorax presents elongate plate on each side of neck, connecting with triangular lobe on posterior rim of head, and with an arm on edge of prothoracic episternum.

2. Prothorax reduced, but all plates present except a preepisternum. Epimerum largest plate. Trochantin does not articulate below with coxa.

3. Dorsal plates of meso- and metathorax (mesonotum and pseudonotum and metanotum and pseudonotum) all fused so that meso- and metaterga are solidly continuous.

4. Meso- and metapleurum (82) alike. One preparaterum (*P*) present in each forming large lobe of episternum. Epimerum fused above with pseudonotum (*PN*).

VII. HEMIPTERA.

Species studied.—*Benacus haldemanum* (83, 84, 85, 86, 87, 88, 89, wing bases 190, 191), *Amorgius americanum*, *Belostomida*.

Characteristics.—The following characteristics may not be general to the Hemiptera, for there evidently exist numerous structural modifications within the order. The drawings of *Benacus haldemanum* can not serve as more than a basis for a comparative study, but they illustrate the agreement of the Hemipteran thorax with the fundamental plan of that in other insects.

1. Microthoracic plates absent.
2. Trochantins (*Tn*) present in each segment, but hidden, together with bases of coxæ, by the produced edges of the pleurites (83, 85).
3. Anterior coxæ articulated to condyls carried by pronotum (83, *CxP*).
4. Posterior coxæ articulated to a condyle of the metaepimerum (84, 89, *k*), which is inserted between the coxa and the true pleural coxal process (*CxP*).
5. Preparaptera not distinct from episternum (85, 89). No postparaptera.
6. Episternum of metathorax divided into an upper and a lower sclerite (89, *Eps*, *Eps*).
7. Scutellum of mesonotum forms a large triangle between bases of fore wings. Mesopseudonotum absent.
8. Metanotum distinctly divided into three transverse parts by transverse lines (87, *pse*, *sct*, *scl*). A pseudonotum (87, 88, *PN*) present, very narrow mesially, expanded laterally where fused with epimera (*Epm*).
9. First abdominal tergum (87, 88, *IT*) a narrow bar fused with metapseudonotum, expanded laterally, bearing the spiracles (*I Sp*) and phragmal arms (*I Ph*).
10. Wing bases shown by 190 and 191. *C*, *Sc*, and *R* form large detached sclerite at humeral angle of hind wing (191) though not detached in fore wing (190). Third axillary divided and of unusual shape in fore wing (190, *3 Ax*), simple in hind wing.

VIII. EUPLEXOPTERA.

Species studied.—*Spongiphora apicidentata* (90–94, 98, 100), *S. brunneipennis* (96).

Characteristics.—This order has been specially studied by Verhoeff (1902, 1903a). The present writer has elsewhere (1908) made a comparison of the Euplexopteran thorax with that of Orthoptera and

Coleoptera. Such a comparison shows many more points of resemblance to the Coleoptera than to the Orthoptera, but at the same time the similarity is of such a nature that it may be secondary rather than phylogenetic.

1. Microthorax well developed, presenting tergal, pleural, and sternal plates (93), one of the latter almost gular in position.

2. Presternum consisting of two plates (*Ps*) in all three segments lying before or beside the anterior angles of the sternum (91, 94, 98).

3. A preepisternum (*Peps*) well developed in mesothorax (94).

4. Trochantin (*Tn*) present in all three segments (91, 94, 98).

5. Propleurum (91) and mesopleurum (94) similar, differing from metapleurum (98).

6. Metapleurum (98) in appearance similar to that of Coleoptera. First preparapterum (*1P*) fused with front of episternum (*Eps*) and bears internally large pronator disc (100, *PD*).

7. Mesonotum (90, 92) simple, mesopseudonotum lacking. Metanotum (96, *N*) complex, presenting median groove fringed with recurved bristles (*G*). Metapseudonotum (*PN*) present, though fused with first abdominal tergum (*1T*).

8. A small rod in wing base connects with parapteral region in mesothorax (90, *n*) and with second preparapterum (*2P*) in metathorax (98, 100, *n*).

IX. COLEOPTERA.

Species studied.—*Calosoma scrutator* (102, 103, 110, 113, 127, 132, 133, wing base 193, 197), Carabidae; *Dytiscus dauricus* (107, 108, 114, 128, 131, 136, wing base 192), Dytiscidae; *Hydrophilus triangularis* (105, 111, 112, 125, 134, wing base 198), Hydrophilidae; *Silpha surinamensis* (106), Silphidae; *Melolontha vulgaris* (117, 121, 135, 138, 139, wing base 195, 199), Scarabaeidae; *Buprestis aurulenta* (95, 99, 104), Buprestidae; *Tetropium glutinum* (123), *Cyllene robiniae* (97, 101, 116, 119, 129, 130, 140, wing base 194), Cerambycidae; *Dendroctonus valens* (118, 120, 122, 124, 126), Scolytidae.

Characteristics.—1. Microthoracic plates rudimentary (95) or absent.

2. Prothoracic and mesothoracic pleura resemble each other more than they do the metathoracic pleurum. Pleurites of the first two vertical or oblique, those of the last horizontal.

3. Prothoracic pleurites commonly fused with each other and with tergum and sternum, but not reduced in size.

4. Mesothoracic pleurites (97, 101, 102, 105, 106, 107, 109) always distinct, usually oblique. Wing process (*WP*) often hidden by prominent upper end of episternum, but easily seen on inner surface (101, 103, 108) as is also its relation to pleural ridge (*PR*). Epimerum (*Epm*) commonly with a dorsal subdivision (*epm*), and

episternum (*Eps*) often divided into several parts by vertical ridges or lines (102, 109).

5. Metathoracic pleurites horizontal or nearly so (110–121). Wing process (*WP*) a prominent oblique arm arising from anterior ends of pleurites, lying just behind and parallel with a similar arm from the preparapтерum which also takes part in supporting the wing. (See description under 8.) Usually a more or less prominent supraepimeral plate present (111–121, *epm*) to which the ends of the metapseudonotum are connected.

6. Trochantin (*Tn*) present in prothorax and mesothorax, but is usually a small sclerite at base of coxa (99, 104) concealed in coxal cavity formed by projecting pleurites. In Silphidae (106) and Buprestidae (109) it is exposed on surface of mesothorax. Lacking in metathorax.

7. Only one preparapтерum (*P*) present in either segment. Postparapтерum lacking. Preparapтерum of mesopleurum usually a small plate or rod lying before the wing process (102, 103, 107, 108). Sometimes it bears a pronator muscle disk (101, *P*, *PD*).

8. Preparapтерum of metathorax in most beetles fused with an anterior subdivision (*eps*) of episternum (*Eps*) as in *Cyllene* and *Dendroctonus* (116, 118, *P*+*eps*), making, with the wing process (*WP*), two conspicuous wing-supporting arms. In lower forms, like *Calosoma* (110, 113) and *Dytiscus* (114, 115) the parapтерum (*P*) and its disc (*PD*) are entirely free from the episternum (*Eps*) though closely articulated to front of wing process (*WP*). Other forms, such as *Hydrophilus* (111, 112) and *Melolontha* (117, 121), show an intermediate condition in which the line of fusion is distinct.

9. Mesonotum (125, 127, 128, 129) generally presents a triangular scutellar area between bases of elytra. Mesopseudonotum lacking unless represented by two small plates (127, 128, 131, *q*) connecting mesonotum with metanotum.

10. Metanotum in lower families like Carabidae (132) and Dytiscidae (136) distinctly divided into three transverse parts (*psc*, *set*, *scl*). The first or prescutum (132, 136, *psc*) carries the prephragma (*Aph*) and the anterior notal wing processes (*ANP*); the second or scutum (*set*) is divided transversely into an anterior and a posterior plate by a large transverse ventral ridge (133, 137, *w*) peculiar to the Coleoptera and forming lines (132, 136, *w*) on the surface, while each of these is divided again into separated lateral regions by a median interlocking of the prescutum (*psc*) and scutellum (*scl*). Thus the scutum consists of four well-marked subdivisions, the posterior pair of which carries the posterior notal wing processes (*PNP*). The scutellum (*scl*) consists of a median triangular area produced into a tongue on the floor of the median notal groove (*G*), formed by the entodorsum or ventral V-shaped ridge (133, 137, *V*),

and of two slender lateral strips forming the posterior margin of the notum and ending in the axillary cords (*AxC*).

This simple *Calosoma-Dytiscus* plan (132, 136) is distorted by modifications in the higher families, but a serial change can be traced through *Hydrophilus* (134), *Melolontha* (135, 138), and *Cyllene* (140).

11. Pseudonotum of metathorax (*PV*) well developed in all beetles (132-137, 139, 140), carrying the postphragma (*Pph*) and articulating by its extremities (*i*) with epimera of metathorax. Absent in Coleopteran pupæ (122, 123).

12. Elytra (*El*) articulated to mesothorax by the ordinary three axillary sclerites, though the first and second are sometimes fused (127, 128).

13. Wing bases of usual construction (192, 193, 194, 195, 198). Head of the costa (*C*) frequently separated from main shaft of the vein (197) and attached to the subcosta (*Sc*) by a process fitting into a cavity in the head of the latter. Venation poorly developed (196). Axillaries normal, sometimes with a small accessory piece (199).

X. NEUROPTERA.

Species studied.—*Corydalus cornuta* (142, 143, 144, 145, 147, wing bases 200, 201).

Characteristics.—1. Posterior segment of guda projects beyond rim of head and is entirely surrounded by membranous sutures, thus strongly suggesting a microthoracic origin. Between head and prothorax is a wide collar-like band open dorsally, mostly concealed within rim of pronotum. Perhaps this collar is microthoracic, but possibly it is presternum of prothorax.

2. Prothorax elongate, depressed. Notum and sternum separated by wide infolded pleuro-tergal membrane. Pleurites reduced to small plates, episternum fused with sternum. Procoxa simple, cylindrical, not double as in meso- and metathorax.

3. Meso- and metanotum sufficiently shown by figs. 142 and 143. Both notal wing processes carried by scutum.

4. Meso- and metapleurum of the adult similar (147). One prepapapterum (*P*), fused with episternum. Trochantin (*Tn*) large. Coxa of two parts, a ventral segment (*Cx*) carrying the trochanter, and a dorsal posterior segment (*epm*). A study of the pupa (145) and the larva (144) shows that the upper coxal segment is simply a detachment of the epimerum (*Epm*) fused upon the coxa (*Cx*). In the larva (144) epimerum is divided (*Epm*, *epm*); coxa (*Cx*) is simple, as in prothorax of adult. In pupa (145) lower subdivision of epimerum (*eps*) extends downward and attaches to rear side of coxa. In adult (147) this separation completed and lower plate (*epm*) of epimerum (*Epm*) entirely detached from the latter and intimately fused with coxa.

This double nature of the meso- and metacoxæ is common to Neuroptera, Mecoptera, Trichoptera, and Lepidoptera, and it has often been adduced as evidence of the double nature of the entire segment. Since, however, it can be shown in all these orders to be a purely secondary adult character, it is evident that it has no such significance whatever.

5. Wing base very simple in the pupa (141). Articular elements and bases of the veins of typical shape in adults (200, 201).

XI. TRICHOPTERA.

Species studied.—*Neuronina ocellifera* (146, 148), *Platyphylax subfasciata*, *P. designata*, larvæ and pupæ of unknown species.

Characteristics.—1. Only one preparapтерum (148 *P*) present, fused with episternum. Pronator disc carried by upper edge of episternum.

2. Trochantin (*Tn*) of meso- and metathorax crowds episternum (*Eps*) from coxal articulation.

3. A wing of the meso- and metasternum (*S*) extends dorsally before the trochantin (*Tn*) to the episternum (*Eps*).

4. Meso- and metathorax similar to each other in size and structure.

5. Meso- and metacoxæ (*Cx*) of adult with a posterior segment (*epm*) as in Neuroptera. This can be shown by a study of the pupa (146) to be a detached piece (*epm*) of the *epimerum* (*Epm*), which has extended downward behind the coxa and fused upon it.

The Trichoptera stand in a position intermediate between the Neuroptera and the Lepidoptera. The resemblance of the Trichopteran pleurum to that of a generalized moth like *Phassus* (149) is very striking.

XII. LEPIDOPTERA.

Species studied.—*Phassus argentiferus* (149, 150, 151, 152, wing bases, 202, 203), *P. triangularis* (153, 154), Cossidæ; *Protoparce cingulata* (155–159, wing base, 204), Sphingidæ; *Citheronia regalis*, Citheroniidæ.

Characteristics.—1. Microthorax represented by one or two sclerites on side of neck (152 *mi*, *mi*).

2. Pronotum well developed in lower families (152 *N*); reduced and longitudinally compressed in higher families, often forming two flat lateral lobes which even become constricted at the base into two stalked plates, the patagia. The patagia are specially well developed in *Agrotis*. A comparative study would show them to be simply developments of the notum, and there is no ground for regarding them as homologues of the wings, nor even of the tegulæ.

3. Propleurum narrow (152). Epimerum (*Epm*) specially reduced, generally obsolete. Episternum (*Eps*) prolonged upward as a narrow prenotal band, overlapped by edge of notum.

4. Prothoracic coxa not articulated to true coxal process, but to a small detached plate in *Phassus* (152 *p*) which in *Protoparce* and *Citheronia* is fused with lower end of episternum.

5. Meso- and metathoracic coxæ (149, 153) double in adults as in Neuroptera and Trichoptera, consisting of an anterior true coxa (*Cx*) and of a posterior plate (*cpm*), undoubtedly derived from the epimerum (*Epm*) as in *Corydalis* and *Neuronina*. The coxæ have but little motion upon the pleurum and the principal movement of the base of the leg is in the articulation between the coxa and the trochanter.

6. Trochantin present in both meso- and metathorax (149, 153, 154, 158, 159, *Tn*), but more or less completely fused with episternum (*Eps*) above, and always closely attached to a wing of sternum (*S*) in front. This is exactly the same as in *Corydalis* (147) and *Neuronina* (148). Lower end sometimes projecting as a free point articulating with ventral rim of coxa and sometimes obsolete.

7. Only one preparapterum present (149, 153, *P*), and it is fused with episternum. Pronator disc (154, *PD*) carried by upper edge of episternum.

8. The pleural wing process of mesopleurum (153, 154, 159, *WP*) bears a large anterior arm (*tg A*) serving as a prop for the tegular plate of the notum (150, 156, *tg*).

9. Mesothoracic notum (150, 156) distinctly subdivided into a presutum (*pse*) carrying the prephragma (155, *Aph*), a scutum divided into two lateral lobes (*set*, *set*) carrying the anterior notal wing processes (*ANP*) and, in *Phassus*, the posterior processes also (150, *PVP*), and into a scutellum (*scf*) forming a posterior triangle (*scf*) whose lateral angles terminate in the axillary cords (*AxC*). Probably in most families the posterior notal wing processes (*PNP*) would appear to belong to the scutellum (*scf*) as in *Protoparce* (156).

10. Tegulae greatly developed in mesothorax (149, 150, 202, *Tg*) and attached to a special tegular plate of the notum (149, 150, 156, *tg*) supported by the tegular arm (153, 154, 159, *tg A*) of the wing process (*WP*).

11. Metanotum in lower forms like Cossidae (151) similar to, though smaller than, the mesonotum (150). In higher families it becomes very much shortened antero-posteriorly, as shown by *Protoparce* (157), and greatly reduced in proportion to the mesonotum (156).

12. A pseudonotum (*PV*) present in both meso- and metathorax, though depressed and mostly hidden (149). In mesothorax (150, 156, *PV*) it carries a large postphragma (*Pph*). In metathorax (151, 157) postphragma (*Pph*) is smaller and fuses with first abdominal tergum (149, 151, *IT*).

13. In wing base (202, 203) media (*M*) and cubitus (*Cu*) fuse with base of radius (*R*). Axillaries of ordinary structure (202, 203, 204).

14. The jugum (202, *Ju*), present in lower families, is simply a lobe of anal region of fore wing and is supported by last anal vein (3*A*).

15. The frenulum (204, *Fr*) consists of a spine or bunch of bristles developed on enlarged base of costa (*C*) of hind wing.

XIII. HYMENOPTERA.

Species studied.—*Cimbea americana* (161–166, wing base 205), *Parasiloba* sp. (160), Tenthredinidæ; *Sirex flavipennis* (161, 171, 172, wing bases 206, 207) Siricidæ; *Pepsis* sp. (168, 169, 170, wing bases 208, 209) Pompilidæ; *Sphæcius speciosus*, Bembecidæ.

Characteristics.—1. Pronotum (*N*₁) attached to mesothorax (160, 163, 169) and but loosely connected with prothoracic pleural parts (160, 162, 168), except in *Sirex* where prothoracic parts retain normal relations (171).

2. Trochantin absent as a distinct sclerite in all three segments.

3. Epimerum of prothorax rudimentary, forming merely a narrow posterior marginal rim on episternum (160, 162, 168, 171, *Epm*).

4. Mesonotum divided into three distinct divisions (160, 161, 163, 170, *pse*, *sct*, *scl*), first of which (*pse*) sometimes entirely concealed by pronotum (169, *N*₁). Scutum (161, 170, *sct*) carries anterior notal wing processes (*ANP*) while scutellum (*scl*) carries posterior wing processes (*PNP*) and axillary cords (*AxC*). Mesopseudonotum (160, 161, 163, 169, 170, *PV*₂) carries large postphragma (161, 163, 170, *Pph*) projecting downward and backward into metathorax.

5. Metathorax well developed and of normal shape in *Cimbea* (164) presenting all the principal pleural and tergal parts (*Eps*, *Epm*, *sct*, *scl*, *PV*). In *Parasiloba* (160) parts somewhat larger, but pleural suture (*PS*) almost horizontal. In all higher Hymenoptera (*Pepsis* 169) the metapleurites (*Eps*, *Epm*) are elongate, entirely fused with each other, obliterating the metapleural suture, and continuous with the pseudonotum (*PV*₃).

6. First abdominal tergum (*IT*) in *Parasiloba* (160) somewhat more separated from second abdominal tergum (*IIT*) than from the metapseudonotum (*PV*₃). In *Cimbea* (164) entire first abdominal segment (*IT*) attached to posterior rim of the metathorax and but loosely connected with rest of abdomen (166). In all higher families (*Pepsis* 169) the first abdominal tergum (*IT*) solidly incorporated into metathoracic wall and virtually a part of metathorax, the peduncular constriction occurring between it and second abdominal segment (*IIT*). This is probably the most distinctive character of the